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SITE FACTOR VARIATIONS AND RESPONSES IN TEMPORARY FOREST TYPES IN NORTHERN IDAHO[1]

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INTRODUCTION

The object of the study was to analyze and evaluate the environmental factors which govern the progressional stages of the secondary forest succession in northern Idaho.

When this study began much uncertainty existed regarding the distribution of trees and forest types in relation to temperature, precipitation, and evaporation and regarding their soil moisture and nutrient requirements in this region. Little was definitely known of the conditions which favored good growth and form of trees, or what gave rise to pure as distinguished from mixed stands. Furthermore, more exact and dependable information was urgently needed in connection with timber sale operations, reforestation practice, land utilization, and forest management generally.

For these reasons studies were begun as early as 1912 with a view to obtaining data on the factors of air temperature, humidity, wind movement, and evaporation, and on the more important physical and chemical characteristics of the soil. The measurements of the various climatic factors, and of soil moisture and soil temperature were begun in 1911 and cover a period of 5 years. The study also included the records of germination and survival of native species from 1913 to 1917 at the points where the site factors were studied. Data were also obtained on responses of native nursery-grown trees installed at these locations, which cover a period of twenty years.

The entire project was approved as part of the research program of the Priest River Forest Experiment Station. In 1936 all of the data obtained were collected and written up as a thesis required for the degree of Doctor of Philosophy at Iowa State College.

It must be recognized that in studies of plant growth and development quantitative standards are yet in the making; that the influence of variable intensities of the environmental factors is not fully understood, and that definite responses of the plant are difficult to establish. Factors of site become controlling according to their duration, summation or extremes; and any individual factor either of climatic or edaphic origin may of itself become limiting to one or more species. The investigator must therefore endeavor to learn what influences seem to be dominant or in what phase or period in the plant's development the individual external factor assumes a leading or limiting influence, and what combinations or summations of the environmental entities become significant, both for single species and for groups or associations.

The writer is much indebted to Raphael Zon and Donald R. Brewster, whose inspiration and encouragement stimulated the initiation and continua-

tion of this project; to those who while Forest Assistants in the U. S. Forest Service helped with the daily records and earlier tabulations, particularly Ernest C. Rogers, C. C. Delavan and Dr. T. S. Hansen; and to Dr. J. M. Aikman, of Iowa State College, for his help in the organization of the material and the preparation of the manuscript.

REVIEW OF LITERATURE

A review of the literature bearing on this problem and related subjects reveals that most of the previous studies of site factors or of correlations of these factors with germination, survival, and growth of trees are incomplete. In some studies only climatic factors are considered; in others only edaphic components. The magnitude of the task involved in a complete study of all factors for any one location no doubt explains the limited number of complete investigations.

In a review of the literature on this subject it is important to consider papers which treat of coniferous forests. An effort has been made to group these papers under two heads: those dealing with climatic and those dealing with edaphic factors. In case of the latter the object has been here to dwell on those which indicate a trend and a progress toward our present knowledge in this field.

Nichols (1924) suggests that the environment of any organism may be described as the sum total, or rather as the resultant, of all the external conditions which act upon it. He considers that the influence of the environment upon a plant is expressed most clearly in terms of limiting factors, but that when a process or reaction which is dependent upon the combined activity of several factors tends to be limited by some particular factor, the limiting effect of this factor may be compensated by the relatively favorable effect of other factors. Obvious compensations exhibited are need for increased light or a decreased demand for moisture due to low temperature.

Livingston (1921) emphasized duration and magnitude of the factors when he classified them as exponential indices, and proposed the use of the ratio of the sum of the physiological indices to the sum of the exponential indices, and also of precipitation-evaporation ratios and temperature-evaporation indices.

Palmgren (1926) reminds us that not only the manner of reactions, but also the interactions of factors within their effective limits must be noted. He states that various phytogeographical factors may cooperate in various ways, in various combinations at various times, and, first and foremost, in different relative strengths. Although many factors quite naturally interact intimately and regularly, others influence each other under certain conditions only. In dealing with a given relation in which plants may occur, he says we are often able to point out definite factors which clearly enough have served as absolutely necessary conditions; and when we perceive a particular

mode of occurrence always reappearing under apparently similar circumstances, we may feel justified in considering the phenomena as illustrating a law.

Lundegardh (1925) considers that every stage in the development of a plant not only has its own optimum temperature, but that the position of this optimum is influenced by light, nutrients, and other factors, even the vigor or the reserve of a plant itself. Lethal temperatures are raised or lowered by the influence of other factors of life and growth, and the important physiological processes do not increase regularly with increase or decrease in value of environmental factors.

For the territory of the Rocky Mountains we have reports by Bates (1924), Larsen (1930), and Pearson (1931) who set forth the ranges and requirements in temperature and moisture of most arborescent species. The prairies of northern Idaho may be said to approximate a growing season of 235 days; 201 days to 241 days for western yellow pine; 165 to 201 days for western white pine; 110 to 145 for the sub-alpine trees of Engelmann spruce and alpine fir. The lower limits of annual precipitation for these associations are, in order, given as 9, 15, 22, and 26 inches.

Robbins (1910) has expressed approximate frostless periods of 5 months and 6 days for the desert, 3 months and 6 days for spruce forests. Frostless periods, however, reveal quantitative requirements of native species much less definitely than temperatures above 43 degrees F.

Pearson (1931) minimizes the value of determining the length of the growing season upon the basis of frost-free nights, since some species make their major growth in late spring, when frosts occur almost every night, and most of the native trees and shrubs in Arizona cease vegetative growth long before the first freeze.

Münch (1915) shows that the heat of the surface soil varies with its dryness, looseness, and color. The highest temperature of moist topsoil recorded was 100.4° F., the highest temperature of similar soil when thoroughly dry reached 148.4° F. Damage to seedlings by lesions took place at temperatures of 140° F.

Simi'ar studies have been made with native evergreens by Korstian and Fetherolf (1921), Toumey and Neethling (1923), and Baker (1929). It appears that the maximum surface or near-surface heats tolerated are: Engelmann spruce, 108° F.; western red cedar, 96; grand fir, 123; and Douglas fir, 131. The increased resistance to injury by extreme heat is due to a thickened epidermis, increase in xylem material and endodermis. Bates (1924) believes that the resistance of evergreen seedlings to heat injury varies inversely as their resistance to transpiration. He lists the heat tolerance in this order: lodgepole pine, western yellow pine, Engelmann spruce, and Douglas fir.

The writer believes that a decrease in direct or diffused sunlight may

easily become a limiting factor in the establishment of evergreen seedlings, especially under cover of other trees or shrubs or in the presence of dense herbaceous vegetation. Nevertheless, he is quite certain that the trees concerned in this investigation possess ability to tolerate shade in different degrees and that this ability expresses itself in seedlings as well as in mature trees. The relative light requirements of the seedlings are often in themselves responsible for the mortality of naturally sown seedlings in various locations within forest areas. In support of these statements the investigations of Burns (1923), Shirley (1929), and many earlier workers can be cited.

Bates (1929) in listing the minimum light requirements for six Rocky Mountain species, gives Engelmann spruce 1.1 percent and piñon pine 6.3 percent. He considers that the seedlings differed in their water requirements inversely as their photosynthetic activity under low light intensities. However, since only 2 percent or less of the total water transported upward in the plant is used in carbon assimilation, it is difficult to believe that such small differences are significant.

Toumey and Kienholz (1931) showed that the competition for soil moisture by underground roots of trees is an important cause of decreased growth and even of failure of new seedlings. The soil moisture in the trenched plot was several times greater than in the plot where the roots which entered from the surrounding trees had not been severed.

A study of rainfall is of importance chiefly as it affects available soil moisture. In general, an increase in atmospheric moisture results in greater amounts of available soil moisture and a more hydrophytic vegetation. Sometimes even under abundant rainfall and suitable air temperature periodic deficiencies of water in the soil may, because of the loose structure of the soil, give rise to a xerophytic vegetation. The different degrees of precipitation under which the Rocky Mountain trees grow have been set forth in the papers by Pearson, Bates, and Larsen referred to above.

But mere rainfall data do not tell the whole story, for the depth and duration of snow cover bear a direct relation to soil temperature and the length of the active growing season. Measurements of depth of snow cover prevailing in the northern Rocky Mountain forests, as given by Larsen (1930) show 17 to 50 inches for the prairies, 37 to 76 inches for western yellow pine, 66 to 207 inches for western white pine and associates, and over 200 inches in the spruce-lodgepole pine forests at higher elevations. Delayed melting of the snow cover supplies water to the soil which thus becomes available for the beginning and maintenance of growth in the spring and early summer months. Furthermore, the snow blanket reduces soil temperature extremes and provides protection to bacterial life and to new seedlings and young trees.

Weaver (1914) studied the evaporation in certain northern Rocky Mountain evergreen communities. He gave the cedar association, which is fairly

close to the Idaho cedar-hemlock-white fir habitat, 0.55 percent greater evaporation than that given by Fuller (1912) for the eastern hardwoods of beech-maple. Evaporation in the larch-fir association in Idaho was 20 percent greater than in the cedar. The prairie association showed 150 percent greater evaporation than the cedar forest.

Researches dealing with edaphic factors are many but scattered. Since practically no such research has been done in the Rocky Mountains, we must reason from principles established elsewhere. In this connection it becomes desirable to consider the soil structure, its organic constituents, bacterial and colloidal properties, and their influence on the temperature and moisture relations; also the chemical elements present, particularly nitrogen, phosphorus and calcium, as well as the microorganisms and the effect of these on humus decomposition, acidity, and alkalinity.

Only very recently have major soil groups been proposed for the world by Glinka (1927), who placed the gray forest soils and podzols in the incomplete or endodynamomorphic category.

Burger (1929) and Miller (1923) have investigated forest soils from the standpoint of porosity and water-holding capacity, Burger in Switzerland and Miller in Michigan. Their investigations reveal that forest soils contain more organic material, especially in the upper 6 inches, and are more porous and absorbent than field soils. The ability of bare soil to absorb water is generally less at the surface than in the lower layers. Burger reports absorption of 63.6 percent of their weight for forest soils and only 8.8 percent for grassland soils. Absorption naturally varies greatly according to the type of grass present and the degree of its use. Stewart (1933) has shown that bluegrass pasture soil in the United States ranks not far below forest soils in pore space.

Buckingham (1907) stated that movement of moisture through a column of dry soil probably occurs as a result of diffusion, and that the loss thus occasioned is proportional to the square of the porosity.

Caldwell (1913) pointed out that the reduction of the water content to the point of permanent wilting is the resultant of the action of transpiration versus root absorption. When the water supply fails, there remains in the soil a quantity which is definitely related to the physical constant of the soil.

Heinrich (1875) may be said to have begun our concept of soil structure, root and water relations. He said "Neither the different cultivated plants nor those designated as swamp or sand plants differ in their ability to extract water from the soil." Briggs and Shantz (1912) came to a similar conclusion. Small differences which occur in this respect are exhibited by plant groups such as grain crops, root crops, and weeds. Craib (1929) added that this physical constant or wilting coefficient is in a large measure dependent upon the colloidal properties of soil; and Haig (1929) considered that height growth of the trees which he studied is definitely linked with the colloidal

properties of forest soil. This problem naturally admits of further investigation, which should reveal more definitely what chemical and microbiological properties influence the colloidal properties.

Stiles (1914) stated that the water content links the physical and chemical characters of the soil together, granted that the soil structure controls the water present. He accordingly proposed a humidity coefficient which could be used in the classification of forest soils.

Falconer and Beal (1933) concluded that excess of moisture in the soil tends to favor anaerobic activity; optimum moisture, aerobic bacterial activity. A turn in either direction may be determined by fineness or coarseness of the soil. Leaf litter under evergreen species decomposes at variable rates, and all decomposition activities on the forest floor are hastened by increase in temperature, provided moisture is sufficient.

It appears from numerous investigations, that the activity of microorganisms depends upon the amount of humus and suitable atmospheric factors, and that denitrification does not proceed satisfactorily unless there exist suitable bases which may neutralize the acids originating from the humus. Bokor (1929) recommends a close study of the microflora of forest soils. Such a study presents a more complicated problem in forests than in agricultural soils. In forest soils a greater emphasis is placed upon the carbon-nitrogen ratio and the humus and lime contents.

Falckenstein (1911), Hicock, *et al.* (1931), Waksman, Tenny and Stevens (1928), conclude that the rate of height growth of trees is definitely related to nitrogen content of the soil and the ammonia resulting from action of the microflora on sugars and hemicelluloses present. They consider that in acid soils fungi are the only agents causing such decomposition, aerobic conditions being essential. In neutral or nearly neutral soils the moisture factor is most important in determining the nature of the organisms which develop, the activities of Actinomycetes being limited to dry soils.

Süchting (1927) claims that the bases are necessary in maintaining soil quality; and that in order to improve impoverished soils, acid must be removed and the missing ingredients supplied. Schutze as early as 1871 demonstrated that in German forests phosphorus, calcium, manganese, potassium, and sodium all increase in quantity in soils on the better sites.

Gaarder and Alvsaker (1938) maintain that, in the western part of Norway particularly, nitrogen content is the deciding factor for plants. This element is required chiefly by microorganisms, especially in the process of decomposing humus and litter; and unless the bed-rock and subsoil supply the necessary bases to hold nitrogen in place, heavy rainwater will cause it to leach out. If leaching takes place, the inevitable result is a strongly acid soil. Therefore the mineral components of bed-rock and subsoil are of paramount importance.

Kruedener (1927) on the other hand, states that the forest type classifica-

tion is one of soil moisture, aeration, and character of the upper organic horizon combined with the petrographic, physico-mechanical groups.

It is held by some authors that soil may be mellowed or neutralized by burning, which no doubt is of value in certain northern locations. Fowers and Stephenson (1934) report that the amount of nitrification in forest soils is stimulated by burning, which results in liberation of basic ash materials and thus increases soluble mineral nutrients for some time after the fire. Since burning destroys the top and surface organic matter, repeated and continuous burning becomes harmful. Hesselman (1918) attributed the successful regeneration of spruce in northern Sweden to nitrification resulting from forest fires, for in pure coniferous forests heavy raw humus renders electrolytes immobile and creates high acidity in the upper layers. This condition is unfavorable for bacterial activity and results in decreased nitrification. The release of mineral substances from ash in the form of soluble salts after the fire assists in nitrification. Hesselman concludes: "As a result of this presentation I am by no means an opponent to burning. I assume, on the contrary, that fire has been an important means of retarding the formation of raw humus. . . . Natural regeneration takes place in the absence of this action, but vastly more slowly."

Barnette and Hester (1930) conclude that the quantities of potassium and other ash constituents are somewhat increased by burning. A low pH concentration on burned areas is also believed to be due to burning and the resulting addition of ashes. Burning injured the colloidal and physical properties and later the chemical. Hackmann (1931) discredits the value of nitrogen, lime, and potassium fertilizers for forest soils and states that phosphorus fertilizers have greater value, basic slag being particularly effective. Phosphorus fertilizers, he claims, give best results on soils with pH values from 4.5 to 6.5.

Tamm (1920) writes that in podzolization under evergreen forests in the colder regions aerobic conditions usually exist and iron may serve as a sol, since it is protected by organic colloids. As a result of leaching of bases, the horizon of alluviation becomes enriched with electrolytes, which cause precipitation of iron and aluminum. Iron and aluminum then serve as a cementing material for incrustation, leading to a hardpan formation.

In some studies in this field the belief has been advanced that the type of vegetation on the terrain plays no small part in soil amelioration or acidification. Diebold (1935), however, holds that soils play a greater role than trees in the formation of humus layers. He states that the poorest type of humus layers is found under a natural association of hemlock and white pine on well to moderately drained nonlimestone Till soils and their steep phases; and that the very best type of humus is developed by hardwoods on limestone soils.

Chandler (1937) has stated that hemlock forests tend to deplete bases

present in the surface soil and cause it to become more acid. On the basis of studies carried out in the Adirondacks, Heimburger (1934) stated that the mineral soils showed practically no correlation between lime content and productivity of the types. The "richer" types had generally a higher lime content than the poorer types, but humus in some of the richer types was very acid and showed little relation to productivity. He concluded that in this region forest types were governed more by climate, geologic formation, topography, and drainage.

Whitfield (1933), who obtained data on the acidity of soils in given altitudinal zones in Colorado, gives for the plains a pH varying from 6.52 to 6.99, for the intermediate montane zone 7.41 to 7.69, and for the alpine zone from 5.25 to 5.88. In the plains and the alpine zones the soil at 12-inch depth was more acid than the 6-inch and surface layers, in the intermediate montane zone the surface was slightly more acid (7.41) than the 12-inch samples (7.69).

According to Turner (1938) there are certain definite mathematical correlations between drainage, soil characters, and height growth of shortleaf and loblolly pines; the best correlation was expressed by the slope gradients between 3.5 and 22 percent; the next best correlation was expressed by depth of the B-1 Horizon; and a rather insignificant correlation existed between the clay content in the B-2 Horizon and height growth. Turner concluded that the interaction of several factors is more influential than the effects of any single factor in determining the rate of height growth.

Turner (1936) observes that site indices (based on height growth of trees) could well be correlated with quantitative group combinations of factors as summarized in a specific soil, with a specific slope, but not with any one factor or grade of factors.

LOCATION AND METHODS

The Priest River Experiment Station is situated in the pan-handle of northern Idaho, in the north and south trending Priest River Valley within the Kaniksu National Forest. The general elevation of the valley floor at this point is 2,300 feet above sea level. On the west side the hills are less than 2 miles distant and rise about 2,000 feet above the valley; on the east side the divide rises to a total elevation of 6,000 feet and is 4 to 5 miles distant. The region is uniformly covered with dense forests except for a sloping mountain meadow on the eastern ridge and some scattered patches of cleared land along the main river and its tributaries.

The different forest types occur in altitudinal zones, beginning with a lower belt of western yellow pine *(Pinus ponderosa)*, which in places may reach an elevation of 4,000 feet. This consociation usually gives way at the upper border to the more mesic species of western white pine *(Pinus monticola)*, grand fir *(Abies grandis)*, western red cedar *(Thuja plicata)*, and

western hemlock *(Tsuga heterophylla)*. Other species frequenting this mixture are western larch *(Larix occidentalis)*, Douglas fir *(Pseudotsuga taxifolia)*, and lodgepole pine *(Pinus contorta var. Murrayana)*. At an elevation of 5,000 to 6,000 feet the subalpine forests begin, consisting of Engelmann spruce *(Picea Engelmannii)*, mountain hemlock *(Tsuga mertensiana)*, alpine fir *(Abies lasiocarpa)*, and whitebark pine *(Pinus albicaulis)*.

The western yellow pine is comparatively pure, especially on the warmer sites. It sometimes mixes with Douglas fir and lodgepole pine and western larch on locations with more soil moisture. Within the intermediate belt the western hemlock and the cedar are the most shade-enduring and permanent species, whereas Douglas fir, western larch, and western white pine are temporary. Western white pine occurs chiefly on the northerly slopes, moist benches and flats; and is most abundant on soils which are eventually claimed by the cedar-hemlock association. Western larch appears most often on sandy bench land or on lower slopes, and Douglas fir grows more often on steep slopes, especially toward the upper parts. Engelmann spruce and alpine fir which are naturally at home above the cedar-hemlock zone are sometimes found along the cool creek bottoms or deep sheltered valleys. Whitebark pine occurs on the more exposed sites within the sub-alpine zone.

This investigation is concerned with the successional stages of development within the central belt and the progression toward the final climax, commonly called the cedar-hemlock association.

MEASURING CLIMATIC FACTORS

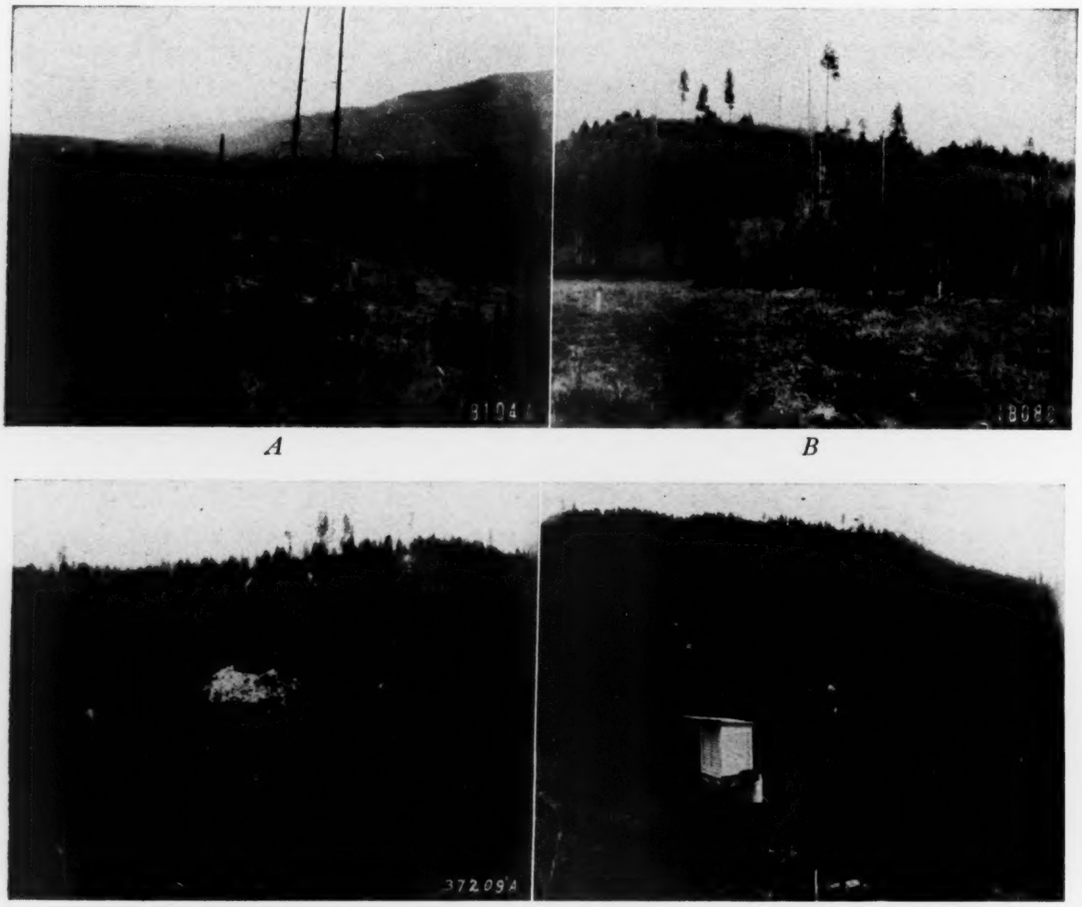
Three main meteorological stations were used in this study: Station 1, on the flat in the larch-fir type; Station 2, on a southwest aspect in western yellow pine; and Station 3, on a northeast slope in a forest composed principally of white pine. There were substations with shorter records: No. 4, on a low flat in the cedar-hemlock-white pine type; 2a, b and c, on steep phase exposed western yellow pine sites; and 3a, on a steep northwest slope in Douglas fir. (See Figs. 1, 2 and 3.)

The station on the flat, Station 1, which served as a control for the others, was placed within a clearing made partly by fire and partly by axe on a sandy bench approximately 100 feet above the main river. This plain has been formed by glacial lake deposits composed chiefly of granitic sand. The land has been burned over twice, about 70 and 40 years before the inauguration of the experiment, and has since been slowly restocking with native trees, chiefly western larch. The earlier fire killed the mature timber and the later one cut big holes in the second growth. Much of the dead and down larger material had been removed for fire wood; and when the experiments were begun, the remnant of debris was removed in order to make room for the station and the various planting tests. Some shrub vegetation has gained a foothold subsequent to the fires, the principal species being mountain balm *(Ceanothus velutinus)*, kinnikinic *(Arctostaphylos uva-ursi)*, nine-

bark *(Physocarpus malveceus)*, june berry *(Amelanchier alnifolia)*, goat brush *(Pachystima myrsinitis)*, and *Spiraea lucida*. (Fig. 1*A*).

Station 2 is on a medium-steep southwest aspect directly north from the flat. The forest consisted chiefly of mature, but very scattered, trees of western yellow pine and a younger understory of mixed yellow pine and Douglas fir. The fire history, destruction and later restocking have developed here along the same lines as on the flat. In addition there existed many clumps of shrubs, chiefly of willow *(Salix scouleriana)*, ocean spray *(Holodiscus dumosus)*, mountain balm *(Ceanothus velutinus* and *C. sanguineus)*, mock orange *(Philadelphus lewesii)*, and ninebark *(Physocarpus malveceus)*. (Fig. 1*B*).

The trees and shrubs combined constitute a topcover of about 50 percent, but of irregular occurrence. In the sub-dominant layer were pine grass



A *B* *C* *D*

Fig. 1. *A*. View south over Priest River Valley. Benton Flat location for Station 1. *B*. Southwest slope, location for southwest slope yellow pine and location for Station 2. *C*. Northeast aspect in white pine and location for Station 3 in clearing. *D*. Northwest aspect in Douglas fir and location for Station 3a. (Near view shows meteorological set-up for Station 2.)

(Calamagrostis suksdorfii), alum root *(Heuchera bracteata)*, Oregon grape *(Berberis aquifolium)*, Indian paint brush *(Castillejia peteolata)*, and lupine *(Lupinus ornatus)*.

At Station 2 fires, heat and wind, typical of western slopes, had reduced the humus layer and favored leaching of the soil, which had resulted in the appearance of shaly fragments near the surface and the absence of any appreciable amount of dark or loamy soil in the A horizon.

The slope reserved for Station 3 is on a 60 percent northeast aspect across the valley of Benton Creek to the east from Station 2. The crest of the secondary ridge is 600 feet above the main valley bottom. There was present on this slope a well developed 70-year-old stand of western white pine, with some western larch and other species. Toward the top of the ridge the stand was chiefly Douglas fir, and from the middle slope downward there was an understory of cedar and hemlock. Evidently the second fire, which 40 years earlier had caused destruction in the second growth on the flat and on the southwest slope, did no damage whatever on this site. (Fig. 1*C*).

On this northerly gradient the soil was 12 to 18 inches deep and loamy with a thick layer of humus and dead needles, but with abundant angular shale fragments which no doubt have become mixed during periods of soil slipping. The reddish brown soil rested directly on a bedrock of shale.

Only under the trees where the light was much reduced were found various sub-dominant evergreens, such as twinflower, *Linnaea borealis, Cornus canadensis*, gold thread, *Tiarella trifoliata;* Clintonia, *Clintonia uniflora*, and wintergreen, *Pyrola bracteata*. On this aspect there was neither natural

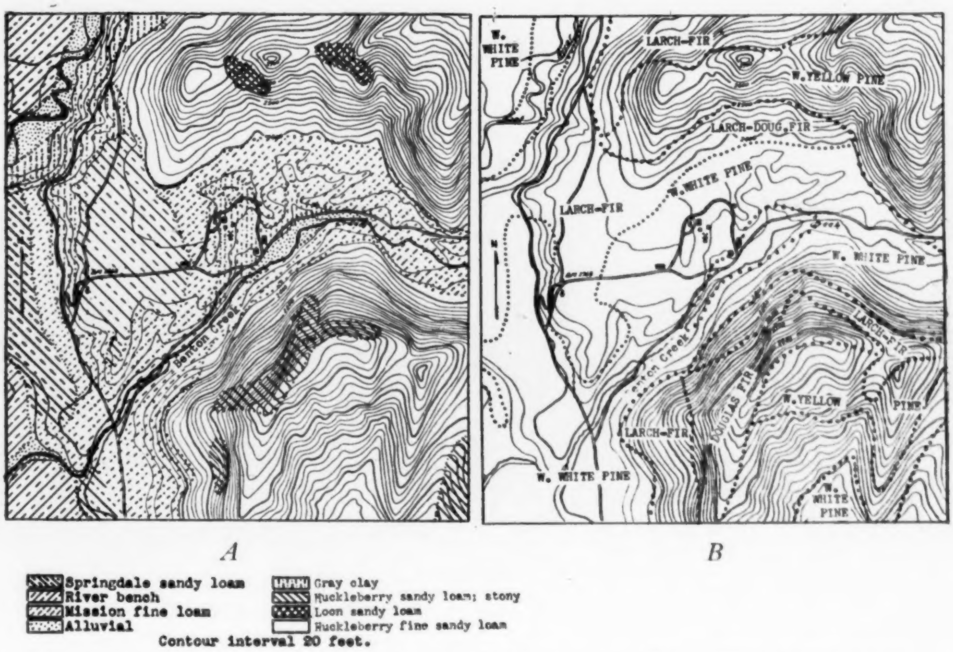


FIG. 2. *A*. Topography and soil types of the area. *B*. Temporary forest types.

clearing nor a shrubby association. A one-acre clearing in the young forest was therefore made. (Fig. 1*C*).

These three locations provided representative sites for the installation of meteorological instruments, soil sampling and the seeding and planting tests.

Sub-station 4 was within a clearing in the 70-year old white pine and larch on a bench having the same elevation as the flat referred to, but nearer Benton Creek. For that reason the soil was silty and compact, quite different from that at Station 1. There was a second growth of western white pine and western larch with an abundant understory of cedar and hemlock. The remaining dead trees and the down timber indicated that the original stand prior to the fire 70 years earlier had contained considerable cedar, with some white pine and western larch. (Fig. 3*A*).

Observations were also made during the growing season of 1915 at another point where the site appeared more extreme than on the southwest

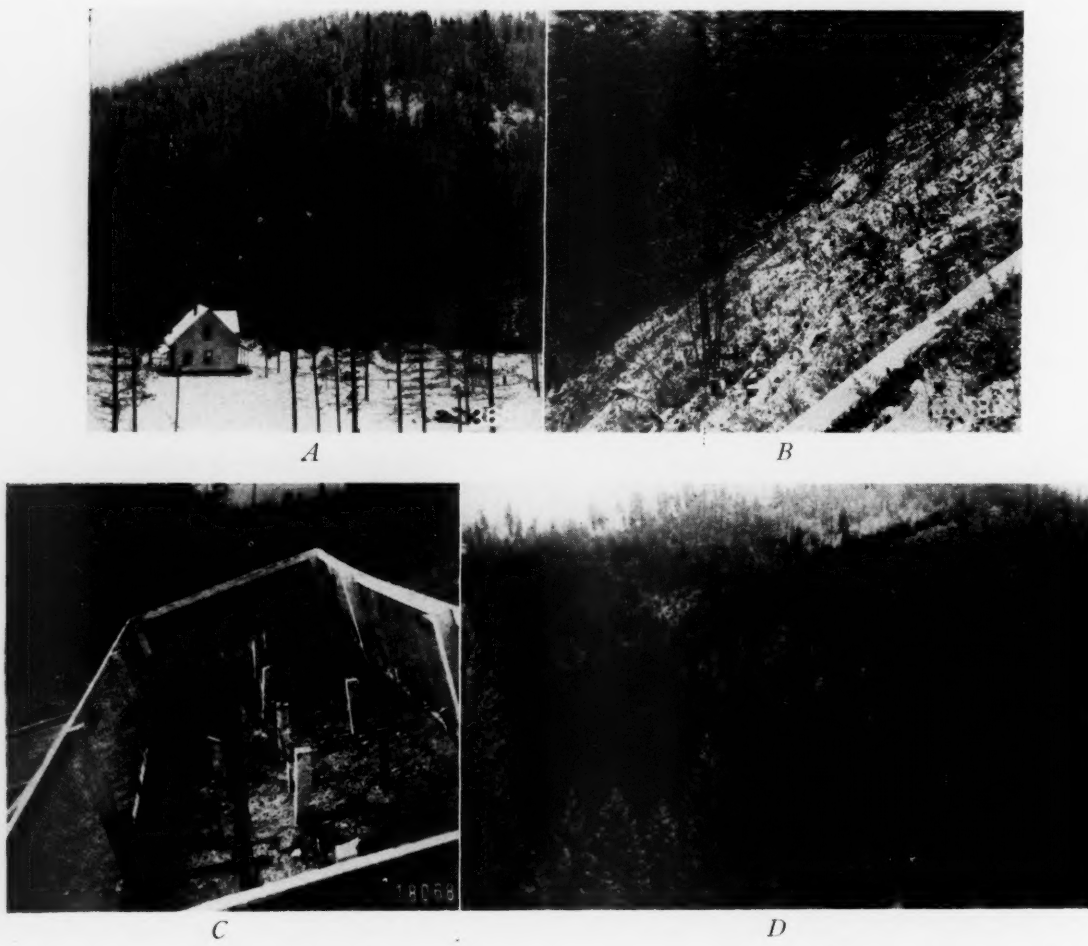


Fig. 3. *A*. Laboratory building and the steep northwest aspect; location of sub-Station 3a. *B*. Details of ground cover and young forest at Station 3 on northeast aspect, 1914; before planting tests were installed. *C*. Seed bed near Station 2 on southwest aspect. The type used for seeding tests. *D*. Steep southerly aspects in open western yellow pine; locations of sub-Stations 2a, 2b, and 2c.

aspect; namely at 2a, on a steep westerly slope. (Fig. 3*D*). During 1915 records were also obtained at 3a, in pure Douglas fir second growth on a steep northwest aspect, on the same secondary ridge, but south from Station 3. (Fig. 3*A*). When the final soil samples were collected in 1932, each one of these sites was represented and several additional locations were chosen for sampling.

The meteorological equipment installed conformed to that used by the United States Weather Bureau. At each station were placed maximum and minimum thermometers of the standard make, a Robinson anemometer and an air thermograph. The stationary instruments were housed in a shelter of the standard pattern, 4.5 feet above the ground. (Fig. 1*D*). (A standard sling psychrometer was used at all of the stations. Each station was also provided with soil thermometers of the maximum and minimum type at the surface, and soil thermometers for readings at 6 and 12 inches below the surface.

In addition to this equipment the station on the flat, serving as a control, was provided with electric contacts for rainfall, sunshine and wind records on a two-magnet meteorograph. The readings of all the factors were made according to mountain time at 5:15 p.m. at Station 3 on the northeast slope, 5:45 p.m. at Station 2 on the southwest slope, and at 6:00 p.m. at Station 1 on the flat.

Air temperature records were obtained at each of the three main stations during the entire five years, and at Station 4 from 1914; and growing season temperature records are available for 1915 for the steep southwest slope (2a) and steep northwest slope (3a). In all cases standard maximum and minimum Weather Bureau pattern thermometers and Friez thermographs were used.

Although all of the hourly temperature records for the entire 5-year period have been tabulated, the unavoidably voluminous data are largely omitted from this report.

Comparative observations on the amount of light within the plant communities were confined merely to a few tests with a Clements Photometer during the growing season of 1913.

Measurements of precipitation embraced records of rainfall and snowfall and of the depth of snow on the ground each day during the season of snowfall, made by use of the standard United States Weather Bureau gauges, checked for durations and intensities by the electric tipping bucket at Station 1.

At the control station on the flat a large Marvin shielded rain and snow gauge was used. This gauge was provided with a spring scale for weighing the amount of rain or snow for each day. The unmelted snow portion was carried into the laboratory where it was melted and carefully measured. Depth of new snow was obtained with the rainfall scale on a canvas mat.

The depth of accumulated snow on the ground was read on the stationary vertical scales at each station.

Relative humidity was measured with a standard sling psychrometer. The pressure column for 27 inches was used in determining relative humidity. No hygrographs were employed at any time. Naturally the low humidity readings which are obtained in the afternoon and the evaporation records carry a much greater significance than readings for the morning hours when temperatures are low and humidity high.

A Robinson cup anemometer mounted 9 feet above the ground at each station provided very reliable wind velocity data. At the control station an electrical connection was made to the office meteorograph, but the hourly tabulated records are omitted because there are no comparisons with the other two sites. (Fig. 1*D*).

The evaporation records, which began in 1914, were made on free water surfaces. From the middle of the summer of 1916, Livingston porous cup atmometers were in use. A comparison of the two methods was continued for some time during 1916.

The free water surface was that of an empty 5-gallon gasoline can set in the ground and painted black and protected by 1-inch poultry netting over the top. Each day the water levels were measured with the rain gauge stick and the water refilled to a line 1 inch below the edge of the can. The amount of rainfall naturally had to be considered in listing the total evaporation for the 24 hours.

Livingston porous cup atmometers were set in the ground to the neck of the jar, and the cup itself was protected with poultry netting.

Measuring Edaphic Factors

The first test of the soils at the different stations dates back to 1915 and comprises mechanical and physical analyses, with ordinary standard soil sieves and laboratory tubes. Most of these early data have been discarded in favor of the more exact analysis of 1932.

The more complete study of soil samples, which included mechanical, physical, and chemical properties, was begun in 1932 and completed in the soils laboratory at Iowa State College. Measurements were made of soil temperature and soil moisture relations in the field during several growing seasons from 1912 to 1916.

Soil moisture determinations are all based on the dry weight; sampling was done by means of a geotome in the undisturbed soil during 1912, 1913, and 1914 and with soil augers in the soil wells during 1916 and 1917. The depths represented are: surface inch; 1 to 6 inches; 6 to 12 inches. The duplicate samples were dried in an oven to constant weight at temperatures not above 110° F.

During 1915 and 1916 sifted local soil was used in one well and sifted sandy loam from station 1 in another. The object in this procedure was to

study more closely the influence of aspect itself on the loss of moisture from the soil. When soil was removed from the wells in sampling, it was replaced by the same kind.

The data on soil temperature were obtained by daily readings at the three main stations from the beginning of the growing season 1913 until the end of 1916. Records were also taken at the sub-stations 2a and 3a during the growing season of 1915. The points at which readings were made are: surface inch, 6 inches and 12 inches. Some records were also obtained during 1912 and 1913 at 24-inch depths.

Surface readings were obtained with standard maximum mercurial and minimum alcoholic thermometers, the bulbs being set within the soil and the rest of the instrument covered with a cedar shingle.

For deeper readings, the mercurial thermometers were set vertical in contact with the ground and within 2 by 2 inch hollow wooden tubes so that the upper end was attached by a string to a wooden plug which closed the bore in the wood. For the 24-inch depth, permanently set soil thermometers were employed.

Some records for 6, 12, and 24 inch depths were obtained during the entire winter of 1915-16. (Fig. 8).

At each point where soil samples were taken in 1932, a canvas was spread on the surface of the ground for mixing the soil. The upper layer of litter and undecomposed organic material was removed and discarded. The spade was then thrust down to a depth of about eight inches, lifting the soil. This was then placed in a heap on the canvas. Here about 50 pounds of soil, taken from four separate pits, were thoroughly mixed with the spade. From this mixture a 2 pound coffee can was filled, covered and shipped to Ames by express on the same day. Another smaller sample was obtained and put in aluminum soil cans and tested for field moisture conditions. (Table 8).

SOWING SEED OF NATIVE SPECIES

This part of the investigation was begun in 1913 by sowing seed of six different native evergreen species in duplicate series on the three main sites. At each of the three main stations there was one seedbed 4 by 12 feet with 12 sub-plots (Fig. 3c): bed A on the northeast aspect; bed C on the southwest; bed E on the flat.

Each was placed in position to obtain the maximum possible light for its particular location.

Each unit experiment consisted of two sets of six plots which measured 2 by 2 feet, or 4 square feet, for each individual test or kind of seed. Six plots in one end of each bed were located on natural undisturbed surface and without removing the grass or litter; at the other end were six plots on which the vegetation was removed by burning. Each plot contained a definite number of seed of a given species. (See Table 15).

Once each week during the first summer after sowing, counts were made

of germination and survival in each sub-plot. At this time the new seedlings were staked out with toothpicks of a given color for each month of germination. The seedlings which had died during the intervening days were removed and the cause of death noted, if determinable. Weekly soil moisture sampling was continued from the initiation of this experiment to the end of 1914, with other moisture determinations later.

In the spring of 1915 each plot which showed seedling survivors was thinned out to a uniform number for all plots so as to obviate competition. From this time until the end of 1917 spring, midsummer and fall counts and observations were made.

Planting Tests

Planting tests were made on the three main sites during 1912, 1914, and 1915. These are described in Series A to D. All the planting was done by two-men crews, one man digging the hole with a mattock and the other setting and firming the plants carefully in the ground. Data on survival and growth and on causes of loss or damage were taken in the fall of 1913, 1914, 1916, 1917, 1919, and 1921, with final height measurements in 1932.

RESULTS

Climatic Factors

AIR TEMPERATURE

The air temperature records have been summarized in Table 1 and shown graphically in Figs. 4a and 5. The data in Table 1 and Fig. 4a reveal that the maxima are higher on the southwest slope than at the other stations, but that the flat is not far below. The northeast slope takes the lower level; there seems to be an absence of hot weather on this aspect. Minimum temperatures at the three stations show much less spread than the maxima and are appreciably lower on the flat than elsewhere. The greatest temperature ranges are found on the flat and the smallest on the northeast slope. The absolute minima are: —29.5° F. on the flat; —20.0 on the southwest; and —17.5 on the northeast. The lowest monthly minima reached during the growth period were 39.32, 43.4 and 44.2° F. in the order given.

Table 1. Summaries of Maximum and Minimum Air Temperatures 1912-1916

Datum	Period	Station 1 Flat	Station 2 SW Slope	Station 3 NE Slope
Averages of monthly maxima	Growth	73.5	74.5	70.0
	Rest	42.5	43.7	41.8
Averages of monthly minima	Growth	39.2	43.4	44.2
	Rest	22.0	25.5	25.9
Means	Growth	56.2	58.9	57.1
	Rest	32.1	34.9	32.9
Average annual range	......	26.2	23.6	18.9
Absolute maxima	......	97.0	99.0	95.0
Absolute minima	......	—29.5	—20.5	—17.5
Extreme range	......	126.5	119.5	112.5

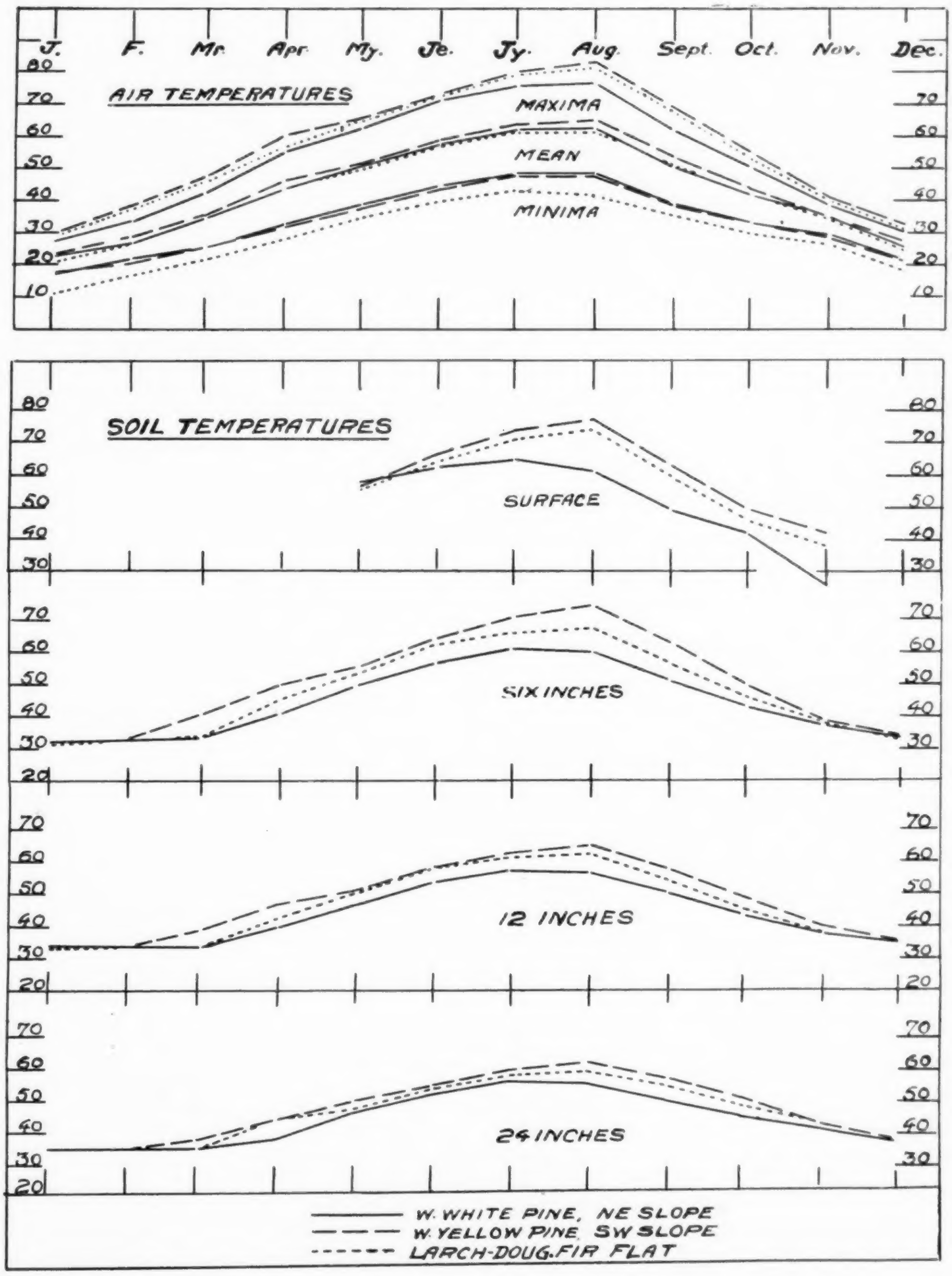


FIG. 4. Air and soil temperatures in degrees Fahrenheit by months.

The thermograph records given in Fig. 5, plotted according to the 2-hour periods, give typical daily oscillations for the three sites and the time at which the highest and the lowest air temperatures occur. From December until February, inclusive, the high points of temperature for all the stations is about 4 p.m., but from this time onward the maximum on the northeast moves forward to 2 p.m., and in August is highest at noon. The digression

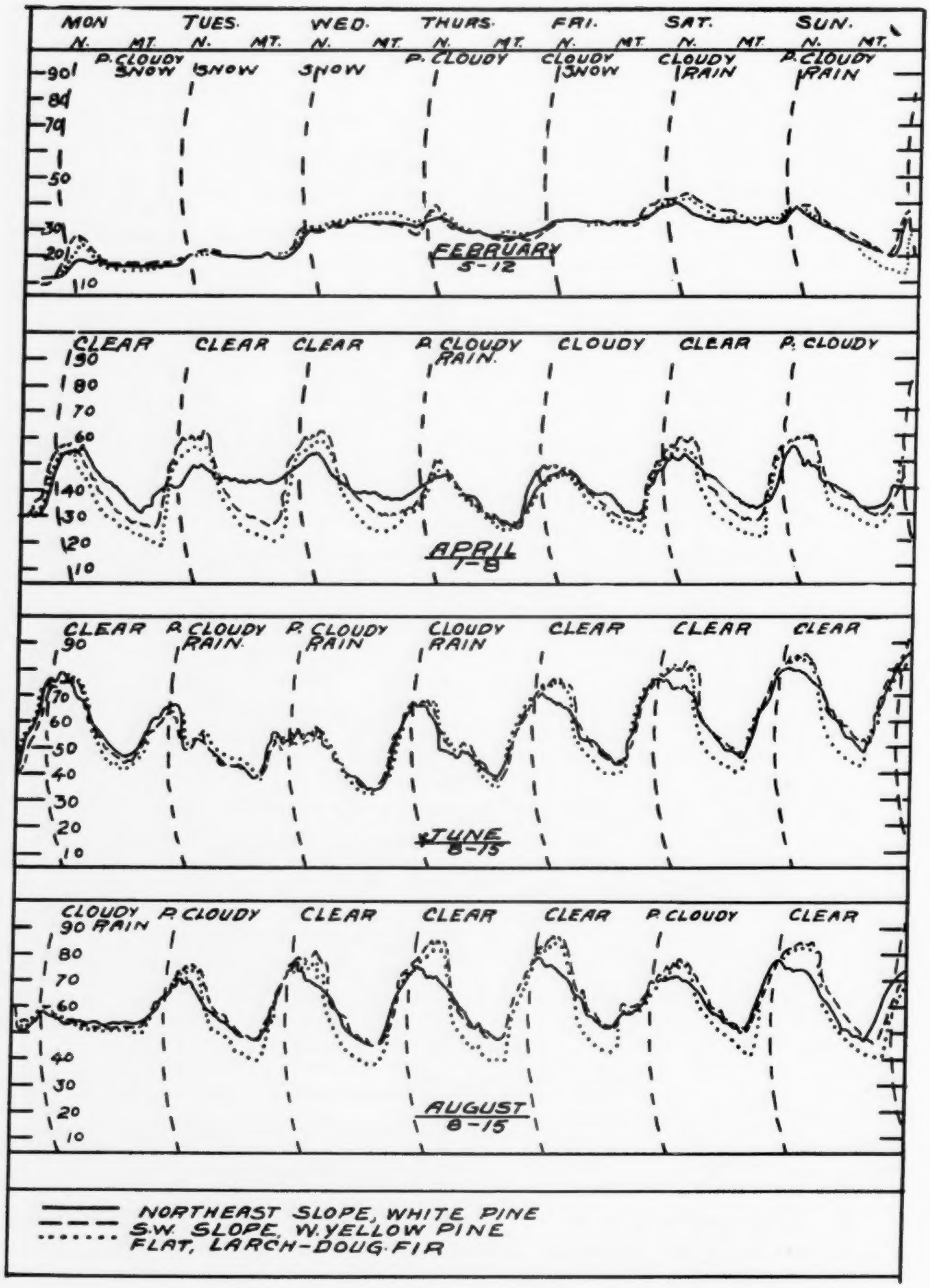


FIG. 5. Typical diurnal thermograph records for selected weeks in 1916.

at Station 3 is due to the position of the sun with respect to the slope and mountain form. At the other stations the extremes of temperature, wind, and relative humidity coincide better.

There is naturally at all the stations a greater diurnal fluctuation in sum-

mer than in winter; but the oscillations are much more pronounced on the flat than elsewhere, and the drop in the minima from midnight until the low point is reached in the morning is practically identical and much less sudden for the two slopes than for the flat. During the colder months, and particularly in cloudy weather, the tendency of the temperature curves is to converge and coincide.

In order to determine how air temperature differences affect the periods of warm, hot or cold days, on the several sites, the days having specific air temperatures of 32° F. and below, 32.0 to 40.0 and 40.1 to 50.0, were singled out. The resulting tabulation showed that the southwest slope actually had 70 more hours of effective temperature (above 43° F.) per growing season than the flat, and 75 more than the northeast slope. There are from 6 to 7 more warm, and as many more hot, days on the southwest slope than on the flat; there are no warm or hot days (above 59 and 72° F.) whatever on the northeast, and 13 more freezing days on the northeast than on the southwest slope. This comparison is based on the averages of the maxima and minima and not on the 2-hour tabulations.

In this region frosts have occurred during every month in the year, July and August not excepted. In general, no frost damage to the native vegetation has been noted during the summer months, but occasionally the tender shoots of Douglas fir and western white pine have shown injury by freezing on the flat in the spring. It was found very difficult to establish Douglas fir plantations on the unprotected sandy flat, because of frost injury to the tender shoots, which resulted in the formation of numerous stool shoots and no real advance in height growth. The white pine plantations showed frost injury during the spring of 1918, an unusually dry and cold season.

The total effect of the temperature variations is that the exposed slope corresponds to a lower forest zonation and the north aspect to a higher forest belt in the altitudinal scale. The high maxima recorded on the exposed aspects and the accompanying conditions in soil and surface are not tolerated by the more mesic species. The result is pure forest of western yellow pine or this species with Douglas fir and a complete absence of western white pine, cedar, hemlock, and white fir. The low temperature levels recorded for the growing season on the sandy flat are instrumental in preventing artificial establishment of Douglas fir.

LIGHT

Since light was not considered one of the controlling factors in the allocation of the species by site or slopes, very few light readings were obtained. Some observations made in the clearings near the three stations with the Clements photometer during the summer of 1913 are given below (Station 1 was used as the standard):

Table 2. Light Readings

Date	Station 1 Flat	Station 2 SW Slope	Station 3 NE Slope
May 2	1.00	0.89	0.44
July 5	1.00	0.70	0.25
August 27	1.00	1.00	0.47
Standard	1.00	Aver. 0.86	0.38

These few records show that even in the clearing on the northeast aspect light is reduced to about 38 percent of that recorded on the flat. Some readings were obtained also in the shade of shrubbery on the flat and southwest slope and under the young stands of trees on the northeast slope. These values referred to the same standard are in order 0.61; 0.61 and 0.03, with variations 0.30 to 0.80 on the flat; 0.70 to 1.00 on the southwest slope; and 0.02 to 0.05 on the northeast aspect.

To what extent light becomes a limiting factor or a cause in the local tree distribution is difficult to state. It is assumed with confidence that it is of practically no importance in the early establishment of all species except perhaps cedar and hemlock, which are supposed to possess chlorophyll rather sensitive to intense sunlight. These species are therefore at a disadvantage on exposed southerly slopes and are set back by sudden exposure occasioned by clearings. Later in life any western yellow pine trees which start on the north slopes are so weakened through scant foliage and slow growth that they succumb to competition of other trees during the period of most rapid height growth; that is, when the stand is from 40 to 80 years old. Even should individual western yellow pines survive this competition and become a part of the canopy of a mature stand, they would not be reestablished because of lack of flowering and seeding.

The decreased amount of light for northerly slopes will retard development of intolerant trees which may seed and germinate on these sites, especially when mixed with more tolerant trees. Seed production itself is curtailed, under those conditions, even in case of the tolerant species.

Rainfall

The records of precipitation and depth of snow are listed in Tables 3 and 4.

By reference to Table 3 we learn that there is very little difference in the total precipitation for the three sites. The average annual precipitation for the flat is 33.2 inches, for the southwestern slope 31.1 inches, and for the northeast slope 33.9 inches. There is less difference between the sites in the summer months than in the winter, and the greatest divergence occurs in November and March, during the windiest months, and at a time when much of the precipitation consists of snow which is carried about by the

TABLE 3. AVERAGE PRECIPITATION FOR A 12-MONTH PERIOD (BASED ON FIVE YEARS' DATA, 1912-1916)

	TOTAL PRECIPITATION (inches)		
	Control Flat	SW Slope	NE Slope
REST PERIOD			
October	2.8	2.6	2.8
November	5.6	5.3	5.7
December	2.9	2.7	3.1
January	4.2	3.9	4.2
February	2.4	2.3	2.5
March	2.6	2.4	2.7
April	2.1	2.0	2.1
Average	22.6	21.2	23.1
GROWTH PERIOD			
May	2.7	2.5	2.7
June	2.6	2.5	2.7
July	2.1	1.9	2.1
August	1.0	0.9	1.1
September	2.2	2.1	2.2
Average	10.6	9.9	10.8
Year	33.2	31.1	33.9

wind, swept hurriedly past the most exposed places at a low angle to the rain gauge, and settles in eddies on the leeward slopes. The summer differences are caused chiefly by the wind and are possibly augmented by evaporation. Since these differences are very small, and since sufficient moisture falls on all three sites to maintain a good stand of western white pine if other factors are favorable, precipitation is evidently not the controlling factor. It is, however, of great importance in indicating that even greater differences may be expected in mountainous country with topographic features of a larger scale.

Although an equal amount of moisture is precipitated at all of the stations, some of this may not be available on the flat because of downward percolation in the porous soil. An even lesser quantity may become available for plants on the southwest slope because of rapid run-off and high evaporation. These conditions have produced less complete vegetative cover and insufficient humus on the southwest aspect. While there is, therefore, less loss of water by transpiration on the exposed slope than on sites with more profuse plant cover, it is nevertheless true that the scantiness of organic matter reduces the water-holding capacity of this site and the amount of available soil water.

In rating the ability of various species to survive on dry sites as seedlings, it is important to examine the time or duration of extremely low moisture conditions, as these are more critical than mere absolute minima. On the drier slopes western yellow pine may survive by virtue of a high resistance to low soil moisture. It is certain that both the western yellow pine and western larch possess marked advantages over the white pine, firs, cedar, and hemlock in a more rapidly developed tap root.

SNOWFALL AND SNOW COVER

Table 4 gives the 5-year record of the snow cover on the different sites. Often, the first snow of the fall remains on the ground both on the northeast and the flat, but melts on the southwest slope. In the spring, however, there is a fairly constant time interval in the date of disappearance of the snow cover on the three sites. The average date for the southwest slope is March 8; for the flat, March 24; and for the northeast slope, April 6. The duration of the snow cover on the northeast slope is thus 141 days, on the flat 128 days and on the southwest slope only 106 days. This difference occurs mainly in the spring. Three successive periods in depth of the snow cover also occur;

Table 4. Average Depth of Snow at the Three Stations for the Five-Year Period—1912-1916

	Depth of Snow on the Ground in Inches		
	Flat Larch-Douglas Fir	SW Slope Yellow Pine	NE Slope
October 15	0	0	0
October 31	0	0	0
November 15	1.5	1.5	2.2
November 30	8.4	5.5	8.8
December 15	9.3	5.5	9.4
December 31	18.1	9.2	19.1
January 15	25.1	18.5	27.0
January 31	27.3	16.9	27.8
February 15	26.8	16.5	30.1
February 28	24.2	6.1	24.8
March 15	18.2	0.3	21.3
March 31	7.2	0	12.7
April 15	0	0	1.0
April 30	0	0	0
Average	11.8	5.7	13.2
	Length of Snow Cover (days)		
Average	128	107	141
Maximum	147	133	154
	Average Date of Disappearance of Snow Cover		
	March 24	March 8	April 6

that of accumulation, that when evaporation and melting equals the precipitation, and that of melting. The first period ends January 15, with only slight differences in the depths at the three stations. The second period ends February 15. During the melting period marked differences in depths exist between the northeast and the southwest slopes. The difference in time of melting varies somewhat according to the depth, the time of the last heavy snowfall, and the kind of weather, but is in the main directly attributable to differences in air temperature, wind movement, and amount of insulation caused by aspects, character, composition and density of the forest.

The much shorter duration of the snow cover and its more shallow layer on the southwest aspect under western yellow pine than on the sites with

larch, fir, or white pine, is an important factor in lengthening the growing season for the western yellow pine and in giving greater protection to soils and seedlings under white pine and more mesophytic trees.

RELATIVE HUMIDITY

By reference to Table 5 and Fig. 6 it is seen that the driest air conditions exist on the southwest aspect, and the most humid on the northeast. This holds true for averages and extremes, although differences in the minima

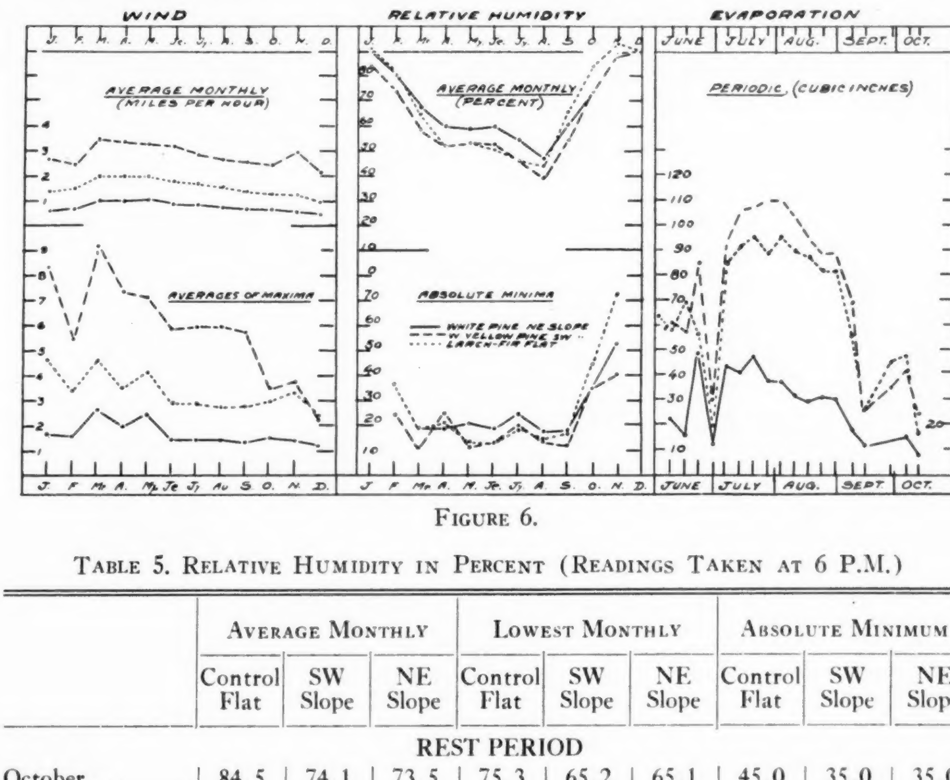


FIGURE 6.

TABLE 5. RELATIVE HUMIDITY IN PERCENT (READINGS TAKEN AT 6 P.M.)

	Average Monthly			Lowest Monthly			Absolute Minimum		
	Control Flat	SW Slope	NE Slope	Control Flat	SW Slope	NE Slope	Control Flat	SW Slope	NE Slope
REST PERIOD									
October	84.5	74.1	73.5	75.3	65.2	65.1	45.0	35.0	35.0
November	93.5	88.8	89.7	91.2	84.9	87.6	73.0	41.0	53.0
December	90.8	89.5	90.0	80.9	87.7	84.2	76.0	43.0	43.0
January	91.7	85.0	90.0	83.8	69.4	79.8	72.0	23.0	46.0
February	82.0	74.0	80.8	79.0	64.0	74.3	40.0	25.0	37.0
March	64.9	59.3	67.6	56.5	49.7	61.3	19.0	11.0	19.0
April	51.9	52.5	60.0	46.4	46.0	47.6	21.0	25.0	19.0
Average	79.9	74.7	78.8	73.3	66.7	71.4	....	....	....
Lowest	....	....	....	....	....	....	19.0	11.0	19.0
GROWTH PERIOD									
May	52.8	53.6	59.2	44.7	43.6	50.1	14.0	12.0	21.0
June	50.8	52.9	60.0	42.8	49.7	57.5	13.0	13.0	19.0
July	46.5	46.0	54.9	36.0	32.3	43.1	19.0	20.0	25.0
August	44.1	38.9	47.1	26.2	23.6	33.0	15.0	14.0	18.0
September	66.2	54.6	60.4	60.8	45.6	56.0	17.0	12.0	18.0
Average	52.1	49.2	56.3	42.1	39.0	47.9	15.6	14.2	20.2
Year	68.3	64.1	69.4	57.8	55.1	61.8	....	....	....
Lowest	....	....	....	....	....	....	15.0	12.0	18.0

registered on the southwest slope and the flat are very small. August marks the climax of the increasing dryness of the air with the progress of the summer, with an average of 44.1 percent on the flat, 38.9 percent on the southwest slope, and 47.1 percent on the northeast slope. But the lowest actual monthly humidity, that is, the month of lowest average in any of the 5 years, indicates the relative severity more accurately than either the 5-year averages or the absolute minima. These values are: larch-fir flat, 26.2 percent; western yellow pine, southwest slope, 23.6 percent; and western white pine, northeast slope, 33.0 percent.

The air on the flat at Station 1 is seemingly more humid in late fall and winter than on the other sites. But this is not true; the discrepancy is due to the later time of reading at Station 1, at a time of the day when the relative humidity increases rapidly with a lowering of the temperature after sunset.

It is, of course, well recognized that through increase in temperature during the day the relative humidity is lowered. This has its influence in creating extremely dry surface and upper soil conditions, especially on western yellow pine and pure Douglas fir sites, a factor or condition which tends to eliminate new seedlings of mesic species.

TABLE 6. WIND MOVEMENT IN MILES PER HOUR

	AVERAGE			AVERAGE MAXIMUM			ABSOLUTE MAXIMUM		
	Control Flat	SW Slope	NE Slope	Control Flat	SW Slope	NE Slope	Control Flat	SW Slope	NE Slope
REST PERIOD									
October	1.3	2.5	0.7	3.0	3.5	1.6	4.0	9.0	2.5
November	1.3	3.0	0.6	3.4	3.8	1.5	4.2	9.2	1.9
December	1.0	2.2	0.5	2.5	2.3	1.3	4.4	10.6	1.7
January	1.4	2.7	0.6	4.7	8.4	1.7	11.2	14.0	2.5
February	1.5	2.5	0.7	3.4	5.5	1.6	5.4	8.4	1.7
March	2.0	3.5	1.0	4.7	9.2	2.7	7.0	11.9	4.3
April	2.0	3.4	1.0	3.5	7.4	2.0	3.7	9.2	2.7
Average	1.5	2.8	0.7	3.6	6.5	1.8	5.7	10.2	2.5
GROWTH PERIOD									
May	2.0	3.3	1.1	4.2	7.2	2.5	5.7	8.7	2.9
June	1.8	3.2	0.9	2.9	5.9	1.5	3.3	6.8	2.1
July	1.7	2.9	0.9	2.9	6.0	1.5	3.7	7.6	2.0
August	1.6	2.7	0.8	2.8	6.0	1.5	3.6	7.6	1.9
Sept.	1.4	2.6	0.7	2.8	5.8	1.4	4.0	8.6	2.0
Average	1.7	2.9	0.9	3.1	6.2	1.7	4.0	3.7	2.2
Year	...	...	...	...	...	...	...	...	...

WIND MOVEMENT

Wind velocity values are given in Table 6 and Fig. 6. As would be expected, the greatest air movement takes place on the southwest slope, where the average per hour both winter and summer is 2.9 miles and the average maximum for any one day in winter is 6.5 miles and in summer 6.2 miles. These average maxima are about twice the movement on the flat and four times

that on the northeast slope. The greatest wind velocities for the control station occur from 2 to 4 p.m., attaining an average movement of 3.2 to 3.9 miles per hour at 2 p.m. and lowering to about one-half mile per hour at midnight or dawn. These records for northern Idaho are very low compared with the other weather stations; in the Northern Rocky Mountains region for the summer months Spokane shows 5.3; Kalispell 4.4; Helena 7.8; and Yellowstone Park 6.9 miles per hour. The sunshine, wind, and moisture deficits fluctuate in close harmony, especially during the summer months; and because each atmospheric factor reaches its peak on westerly slopes in middle afternoon of each day, the high points of several climatic factors coincide and produce critical extremes. The influence of this situation is more keenly felt on the south and west aspects than elsewhere, particularly in July and August. It is here that seedlings of all species perish in great numbers.

TABLE 7. TOTAL EVAPORATION FROM A FREE WATER SURFACE

	Station 1	Station 2	Station 3
	Total Evaporation and Rainfall in Inches, by 15- and 30-Day Periods for 1916		
June 3-30 Evaporation	3.19	3.94	1.71
Rain	3.19	3.11	3.13
July 1-31 Evaporation	4.03	4.48	1.78
Rain	1.66	1.49	1.83
August 1-31 Evaporation	3.52	3.76	0.84
Rain	1.22	1.12	1.27
September 1-30 Evaporation	1.86	2.25	1.39
Rain	1.86	1.80	1.86
	Evaporation from Livingston Porous Cup Atmometer in cubic centimeters per day for 1917		
July 1-15	30.0	....	....
July 16-31	29.3	....	....
August 1-15	26.6	30.0	23.4
August 16-31	27.6	30.0	26.3
September 1-15	12.0	13.1	10.7
September 16-31	16.1	21.2	14.1

EVAPORATION

Evaporation for the month of July, 1916 (Table 7 and Fig. 6), was 4.03 inches for the flat; 4.48 for the southwest slope and only 1.78 for the northeast aspect. Rainfall-evaporation ratios were 2.4 for the flat, 3.0 on the southwest slope, and about 1.0 on the northeast slope. In September, however, the ratios are 1.0 at Station 1; close to 1.3 at Station 2 and 0.8 at Station 3.

EDAPHIC FACTORS

SOIL TYPES

The soil tests made in 1932 were correlated with the soil types distinguished and mapped in 1925 by M. H. Lapman and F. O. Young, of the

Bureau of Chemistry and Soils, United States Department of Agriculture; and the following is quoted from their manuscript notes of 1925 in the Experiment Station files: The names and classifications are not to be considered final. (See Fig. 2.) (Note: arabics are used for the numbers as given by the above authors; numbers are given according to stations and other locations in this study. See Table 9.)

Along the Priest River, Benton Creek, East River and its south fork are low, poorly drained alluvial bottoms, comparatively narrow and of small extent. A little higher are terraces or flats of stream-laid or lake-laid origin. These are somewhat eroded and rolling in places, but are for the most part flat.

The upper boundaries marking the edge of the old lake occur just above 2400 feet elevation in most places. Arms of the lake extension reach up along the various creeks which drain the area. . . . The deposit is many feet in thickness; . . . the soil has a smooth to lightly rolling surface. The drainage is generally good, as is the moisture-holding capacity.

The surface soils are remarkably similar in physical characters. . . .

It seems probable that the majority of the soils are somewhat modified by an admixture of loess or fine-floury, wind-borne material. The majority of the soils are remarkably free from horizontal development due to weathering; the subsoil being generally friable and free from marked compaction except in types 14 and 54.

The soil at Station 1, Benton Flat (No. 6), is Springdale sandy loam supporting western larch and some Douglas fir on the edges of the flat. On this flat the sand and gravel are very deep and well sorted, leading to the supposition that lake water, possibly of glacial origin, was instrumental in its formation. Some pits were dug to depths of 7 and 8 feet without striking clay or bedrock.

At Stations 2 and 3, the soil (No. 9 on the map) is Huckleberry fine sandy loam supporting a mixed stand of western yellow pine and Douglas fir on the southwest aspect and mainly white pine on the northeast. This is one of the most important, and by far the most extensive, soil type in the area.

It is a residual soil from schists and quartzites which occur in alternating layers overlying the granite which forms the backbone of the range to the east. The surface soil consists of 12 to 18 inches of light reddish brown fine sandy loam . . . and usually contains a large percentage of gravel or rock. This soil mantle is of a good depth but small patches of rock outcrop are of frequent but irregular occurrence. The steeper phases are generally more shallow and stony. This is particularly true of the steeper phases at 2a.

At Station 3a the soil (No. 31) is also a steep, stony phase of No. 9, derived from the same parent material. At Station 2a there is also a mantle of Huckleberry fine sandy loam covering a steeper, more stony surface without humus or litter except under the scattered clumps of evergreen shrubs.

The soil (No. 54) at Station 4 is gray clay . . . consisting of a light gray, rather compact heavy clay loam or clay over a light gray compact clay subsoil. It is the same lake-laid material which forms the subsoil of the Mission

fine sandy loam. The surface soil when exposed is apt to pack and bake into a rather impervious condition, and this may render it difficult for young trees to get a start. Once established, however, timber thrives, and a protective cover of duff prevents baking and helps to absorb moisture which might otherwise run off. The surface is generally somewhat rolling or sloping as the material is exposed along the terrace slopes. The surface drainage is somewhat excessive, though the sub-drainage is slow. In moisture holding this soil rates very high.

It supports the more mesic of the forest associations; western red cedar, hemlock, and white fir, as well as western white pine.

Soil type 14 (4a) is a fine sandy loam, which is compact, friable, light brown or yellowish brown fine sandy loam and distinctly micaceous. The subsoil of gray clay with rusty particles occurs at a depth from a few inches to two feet. This clay subsoil is apparently a part of an old lake deposit, the remnants of which are found in a number of places in the vicinity.

SOIL PROPERTIES

The mechanical analyses of the soils made at Priest River in 1915 are given in Table 8, and all essentials of the mechanical, physical, and chemical study made at a later date have been entered in Tables 9 and 10.

The mechanical analysis data given in Table 8 reveal the stony nature of the southwest and northeast sites, the first of which contains mostly western yellow pine, and the second pure Douglas fir. There is present in the soil at these two locations very much less of the finer material than is found where white pine thrives. In this series of tests 56 per cent of the total weight of the sample from the northeast white pine site passed the one-half millimeter sieve and 67.6 percent from the white pine-cedar hemlock flat at Station 4.

By the mechanical analysis given in Table 9 it is well demonstrated that the soil which supports western white pine, with cedar and hemlock, contains a greater clay fraction; and that where Douglas fir and western yellow pine grow, the soils have a correspondingly higher sand fraction. The amount of silt increases under the hydrophytic species and is present in smaller degrees under larch, Douglas fir, and western yellow pine.

TABLE 8. MECHANICAL ANALYSIS OF SOILS BY SIFTING (TESTS MADE AT PRIEST RIVER STATION IN 1915)

Location	Soil type	Percent Passing Mesh by Weight						Total used
		5 mm.	4 mm.	3 mm.	2 mm.	1 mm.	½ mm.	
Station 1; Flat	6	9.2	5.1	5.9	12.9	27.6	39.3	272
Station 2; SW Slope	9	24.5	5.2	4.2	15.0	5.6	45.4	261
Station 3; NE Slope	9	26.5	3.4	3.0	3.4	4.3	59.0	233
Station 3a; NW Slope	31	38.5	6.8	4.4	9.2	9.7	30.7	293
Station 4; Flat	54	1.9	1.9	6.2	10.5	11.9	67.6	210

TABLE 9. MECHANICAL AND CHEMICAL PROPERTIES OF THE SOILS (BASED ON A STUDY OF SOILS TESTED IN 1932)

Station No.	Map No.	Location	Soil Type	Forest Type	Sand	Silt	Clay	Carbon	Organic Matter	Total N.	Phosphorus	pH
					Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	
1	6	Benton flat	Sandy loam	Larch-fir	62.43	19.54	18.03	1.405	3.422	0.1114	0.1422	6.72
2	9	SW slope	Fine sandy loam	W. yellow pine	50.99	33.61	15.40	2.142	3.693	0.0084	0.1070	6.22
2a	9	SW slope	Fine sandy loam (steep phase)	W. yellow pine	36.18	47.93	15.89	0.577	0.994	0.0825	0.0739	6.89
3	9	NE slope	Fine sandy loam	W. white pine	30.98	32.78	26.50	1.430	2.465	0.1061	0.1455	6.98
3a	31	NW slope	Sandy loam (stony phase)	Douglas fir	39.14	36.18	24.68	1.261	2.174	0.0803	0.1016	7.02
4	54	Moist flat	Gray clay	W. white pine, cedar, hemlock	17.39	35.01	47.60	1.049	1.809	0.0889	0.2069	6.75
4a	14	Low SW slope	Fine sandy loam	Larch-white pine	32.03	39.09	28.88	1.306	2.251	0.0754	0.1472	6.37
4b	18	River bench	Clay loam	White pine, cedar, hemlock	14.39	53.41	39.02	2.315	3.990	0.1259	0.2872	6.52
5	—	River flat	Clay loam	Old W. white pine	12.53	54.10	33.37	1.745	3.008	0.0972	0.1598	6.02
6	—	Rolling land	Sandy loam	Old W. yellow pine	37.13	29.35	33.52	1.259	2.176	0.0918	0.1254	6.68
7	14	Podzol	Over-fine loam	W. white pine	19.73	54.16	34.43	3.030	5.220	0.1550	0.0825	6.34

At Station 2, on the southwest aspect, the physical soil characters are intermediate, and here we observe that occasional Douglas firs grow in mixture with the yellow pine. At Station 2a (steep phase SW slope) the clay

fraction is very low and all of the other physical characters are strikingly similar to those found under the old yellow pine forest represented in Table 9 by number 6.

The soil of the Benton Creek flat (No. 54) surrounding Station 4, and that of the virgin forest of western white pine in Station 5 are very similar to the other mesophytic sites measured, both of them showing heavier portions of silt and clay. A comparison of 2, 2a and 3, which are derived from the same parent rock, but now resting on different aspects, reveals no appreciable variation in the sand and the silt portions, but a much greater clay fraction in the mantle under the white pine forest on the northeast slope. Western yellow pine, Douglas fir, and larch appear on lighter soils.

CHEMICAL PROPERTIES OF THE SOILS

Data on the chemical relations of the soils are given in Table 9. In general, wherever one chemical element is low, as on the more xeric sites, the

TABLE 10. WATER RELATIONS OF THE SOILS

Soil Number and Station Aspect	Soil Type	Forest Type	Water Relations: Saturation	Holding	Capillary	Gravitational	Hygroscopic	Wilting Coefficient
			Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
1 Flat	Springdale sandy loam	Larch-fir	50.4	45.05	40.2	10.3	4.85	7.5
2 SW	Huckleberry fine sandy loam	Western yellow pine	70.1	62.02	58.4	11.6	3.62	6.9
2a SW	Sandy loam (steep)	Western yellow pine	50.7	41.48	38.6	12.2	2.88	6.3
3 NE	Huckleberry fine sandy loam	Western white pine	78.7	69.13	62.7	15.9	6.43	10.2
3a NW	Sandy loam (stony)	Douglas fir	65.5	59.65	63.8	11.8	5.85	10.2
4 Flat	Gray clay	Western white pine, cedar, hemlock	74.3	59.85	53.8	20.2	6.05	11.3
4a SW	Mission fine sandy loam	Larch-white pine	79.1	73.81	67.9	14.6	5.91	12.1
4b River Bench	Loam	White pine, cedar, hemlock	104.8	96.27	89.8	14.7	6.47	6.7
5 River Flat	Loam	Old white pine	89.7	81.26	74.5	15.0	6.76	9.4
6 Rolling	Sandy loam	Old yellow pine	39.7	35.06	29.4	10.3	5.66	5.1
7 Podzol	Mission fine loam	Western white pine	101.6	56.07	48.4	16.2	7.67	—

other elements are also more limited. Soils of lighter texture and of lower water holding capacity under the xerophytic species carry from one-third to one-half of the nitrogen, phosphorus, and carbon found in the heavier soils. The steep slope at Station 2a and the rather steep northeast site at 2 show a strong contrast: the former with western yellow pine carries only one-third to one-half of the chemical elements present on the white pine slope.

Most soils are mildly acid and show a slight tendency toward greater acidity in the older stands, but not of a nature to prevent humus decomposition or create raw humus. The old-growth western white pine forest soil contains considerably more carbon, nitrogen, and phosphorus than the old-growth western yellow pine.

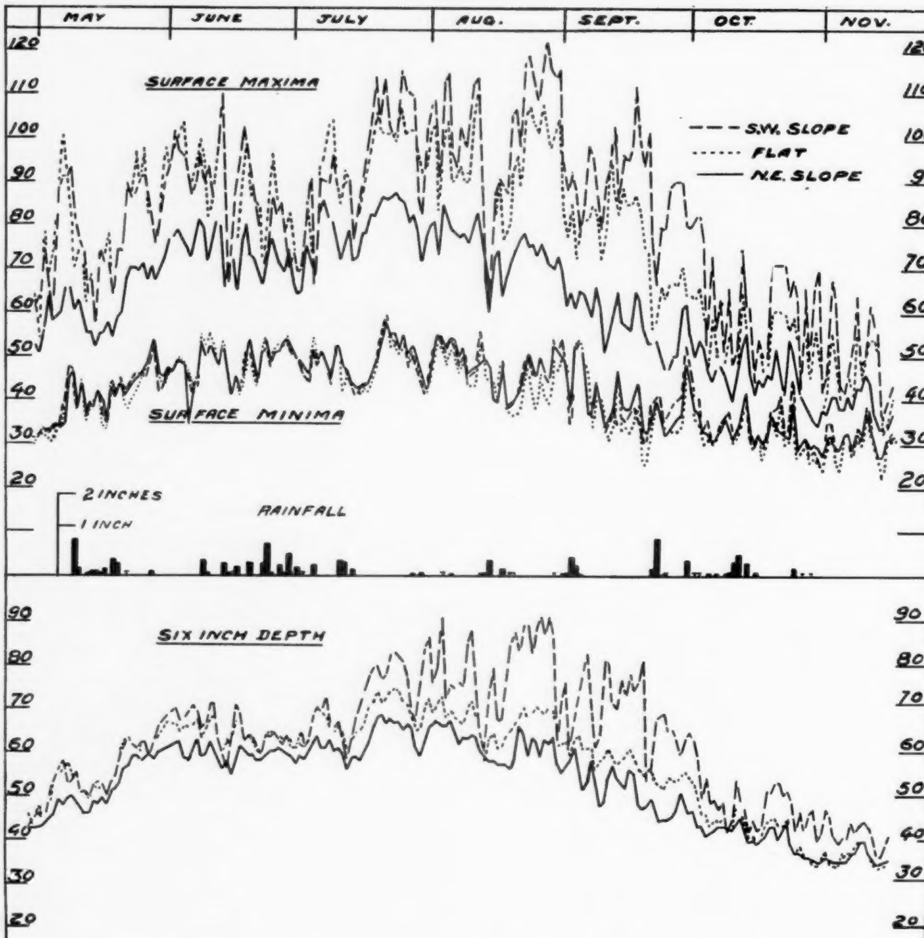


FIG. 7. Daily soil temperatures in degrees Fahrenheit for the period May through November, 1913.

For some years subsequent to the destruction of a forest by fire, the soil may become alkaline especially in the upper layers. This alkalinity stimulates seedling development because of the more readily available nutrients and the absence of competition. Reaction to this advantage appears more vigorously in western yellow pine, western white pine and larch than in the remaining species.

WATER RELATIONS OF THE SOILS

The soil structure influences its water relations to a marked degree. The characteristic water relations of the various soils are given in Table 10. The capillary water, the water-holding capacity, the amount of water required to saturate, the gravitational and hygroscopic moisture, and the wilting coefficients all vary in the same direction, showing greater magnitude for white pine, cedar and hemlock sites (Nos. 3 and 4 and sample 4b and 5), and lowest for virgin western yellow pine. These soil properties are distinctly intermediate for Douglas fir and western larch. The knowledge gained of the different soils by the laboratory tests is corroborated by the field moisture studies given in the section on soil moisture.

SOIL TEMPERATURE

The monthly soil temperature correlations graphs for the several stations are given in Fig. 4b. Records for the soil temperatures obtained in 1913 have been presented in Fig. 7a; data for 6, 12, and 24 inch depths in 1913 in Fig. 7b; and the daily comparison graphs for the entire season of 1915 in Fig. 8. A summation of days having specific soil temperatures has also been prepared (Table 11).

The averages of the surface soil maxima show generally higher values on the southwest slope than elsewhere, although the stations on the flat show nearly as high an average maxima, with occasional higher daily readings.

TABLE 11. DAYS HAVING SPECIFIC SOIL TEMPERATURES AT 1 TO 6 INCH DEPTH, 1912 TO 1916

Season	Station	Freezing	Cold	Cool	Warm	Hot
		Below 32°F.	32.1-40	40.1-50	50.1-60	Above 60°F.
Rest period	1 Flat	34.0	111.5	62.5	5.0	0.0
	2 SW	6.0	122.5	64.5	0.0	0.0
	3 NE	6.0	148.5	57.5	5.0	0.0
	4 Flat	....	146.0	62.0	19.0	0.0
Growth period	1 Flat	0.0	0.0	17.0	79.0	57.0
	2 SW	0.0	0.0	11.0	106.0	65.0
	3 NE	0.0	1.0	45.0	110.5	0.5
	4 Flat	0.0	0.0	26.0	77.0	16.5
Entire year	1 Flat	34.0	111.5	79.5	84.0	57.0
	2 SW	6.0	122.5	75.5	106.0	65.0
	3 NE	6.0	149.5	103.0	115.5	0.5
	4 Flat	....	146.0	88.0	96.0	16.5

The highest surface soil temperature on record on the southwest slope reached the capacity of the thermometer at 125° F.; the extreme temperatures on the flat and on the northeast slope are 118° and 90° F., respectively. The lowering of the curve for the northeast slope in the afternoon is also due to the depression of the angle of inclination of the sun at that time.

In Figure 7a an effort has been made to correlate the maxima and minima of temperatures in the upper inch of soil. The most noticeable feature here is the remarkable uniformity in the daily minima and the pronounced divergence in the maxima. The higher the maxima, the greater will be the spread between the protected and the exposed aspects. On one day, August 27, 1913, this difference reached 45° F. At the close of the season, during late September and early October, the maxima at the different sites became more uniform. The temperatures shown in Fig. 7a have a close bearing on the germination and survival in the seeding tests discussed later.

The lower soil depths ordinarily have less heat than the upper levels in summer and fluctuate more slowly, with a definite lag of one day at 12 inches and two days at 24 inches. At times during the summer when a sudden drop in air temperature takes place, there is a complete reversal of the customary order; the surface soil then has a lower temperature than the soil at greater depths.

At the 6-inch depth and the 12-inch depth, and deeper (Figs. 7b and 8) the southwest slope is shown to be the warmest of the four sites, and the northeast slope the coldest. Temperatures for the lower depth are more moderate, with lesser diurnal fluctuations.

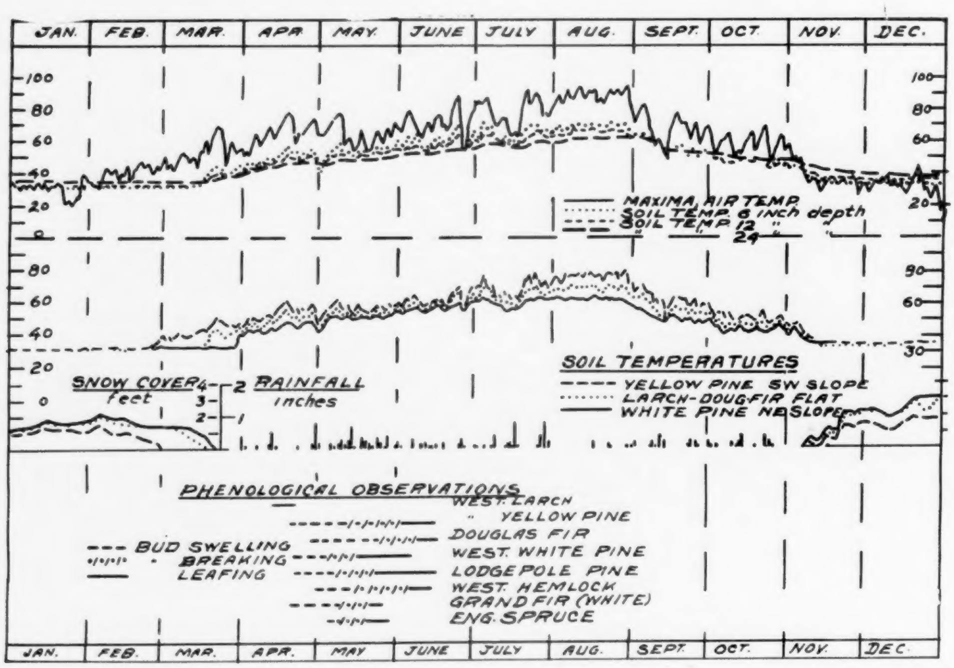


FIG. 8. Relation of air and soil temperature (degrees F.), snow cover, and rainfall.

When discussing soil temperatures it is well to bear in mind that the composition of the soil particles themselves and the water present affect in no small degree the absorption of solar radiation. A large amount of rock, gravel, and sand favor rapid heating, the moister soils responding more slowly. For these reasons the temperature fluctuations of the clay soil on the flat at Station 4 are more like those of the soil on the northeast slope than

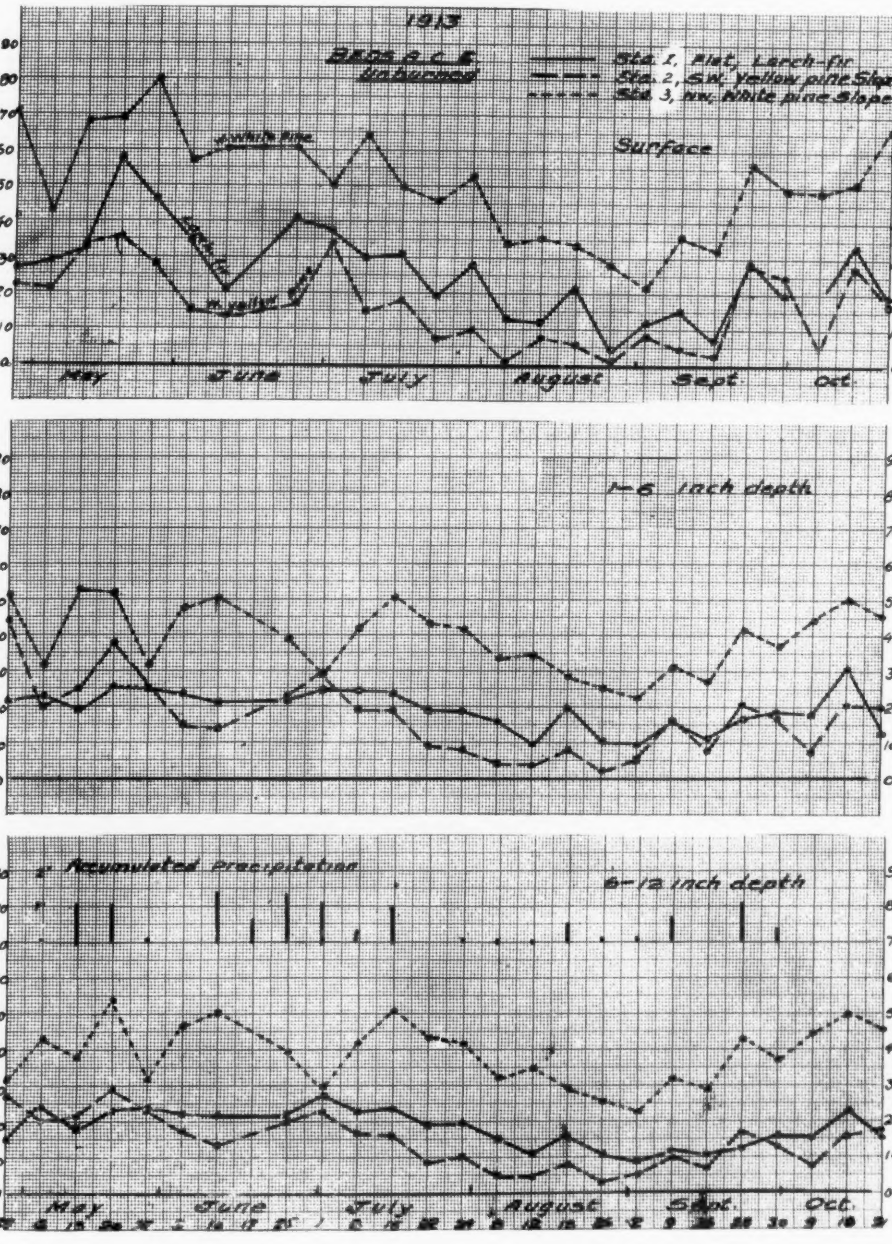


FIG. 9. Moisture content of soils for surface, 6-inch and 12-inch depths at Stations 1, 2, and 3 for the entire growing season of 1914 in unburned ground.

of those on the other sites. The western yellow pine sites show high surface heat and extremes generally, with more even and moderate conditions on western white pine sites.

In Figure 8 we may observe the relations existing between the air temperature and snow cover; the relation of air temperature to the beginning of growth in spring for the different species; and the influence of the daily air temperatures on the heat imparted to the soil at different depths.

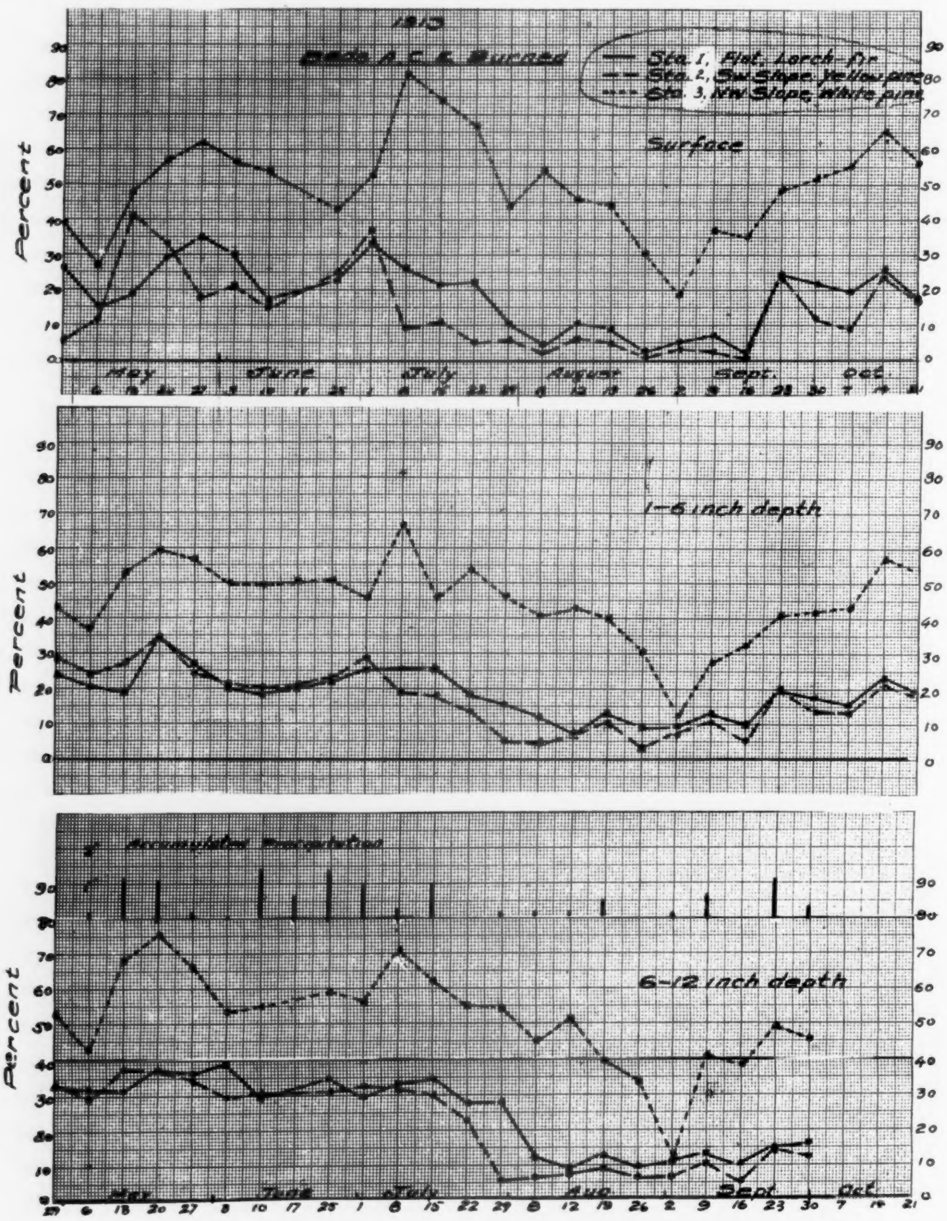


FIG. 10. Field moisture content of soils for surface, 6-inch and 12-inch depths at Stations 1, 2, and 3 for the entire growing season of 1914 in burned ground.

It is observed that no increase in soil temperature is possible before complete snow melting, and that the soil temperature rises almost immediately after the snow mantle is removed. Underneath a snow cover the soil at a depth of 6 inches remains at about 32° F. throughout the winter, but is from 2 to 3 degrees warmer at a depth of 24 inches.

The time of beginning of growth and its relation to air temperature is also given in Fig. 8. This shows the comparatively early start of larch; late beginning of spruce and the intermediate and simultaneous beginning of western white pine, lodgepole pine; with grand fir, Douglas fir, and hemlock last. These records refer to the forest surrounding the Experiment Station buildings and more particularly at altitudes near 2,300 feet. They are therefore related to temperature data obtained on the flat.

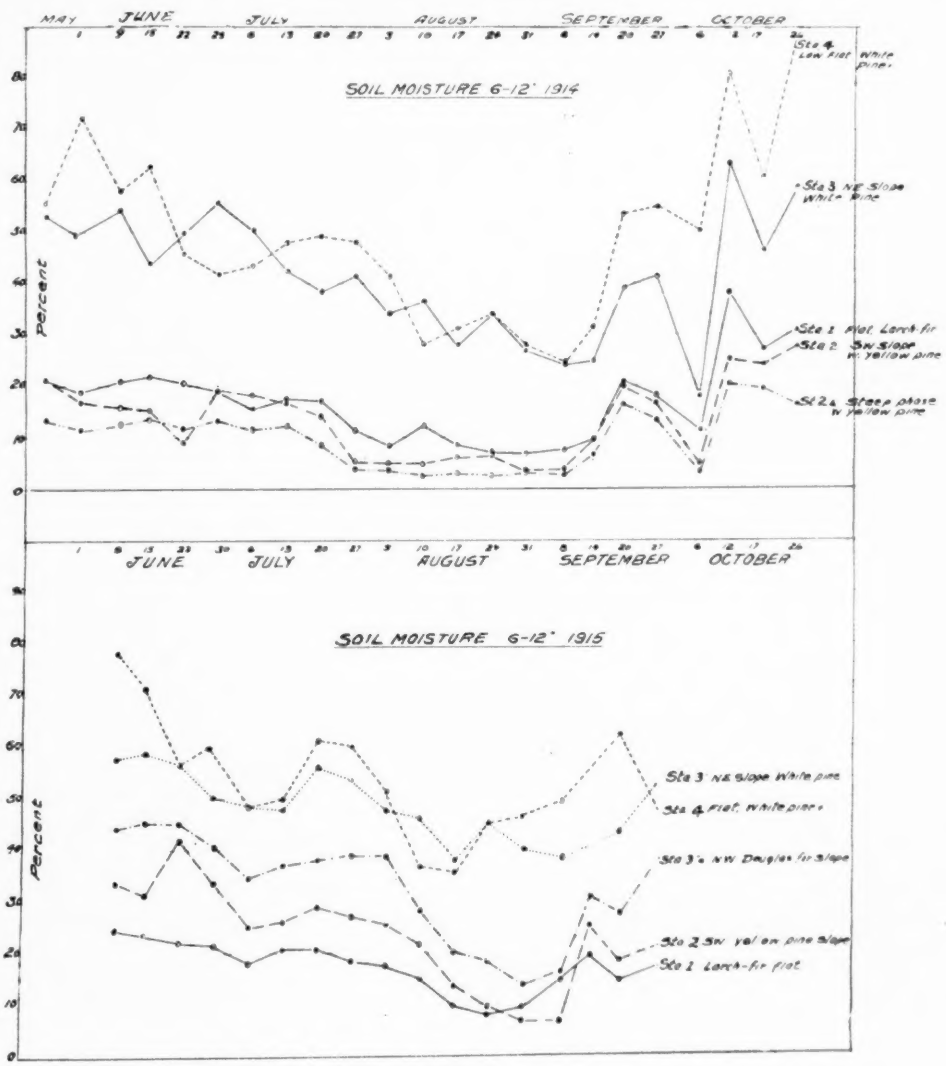


FIG. 11. Field moisture content of soils at Stations 1, 2, 3, and 4 at 6- to 12-inch depths for the entire growing seasons of 1914 and 1915.

FIELD SOIL MOISTURE DETERMINATIONS

Soil moisture data are available largely through field determinations made from 1913 to 1915, inclusive. These are expressed in percentage of dry weight of soil and are given in graphic form in Figs. 9, 10, and 11, the first two for the 1913 season and the last for 1914 and 1915. In Figure 10 are given the three-station relations for surface, 1 to 6 inch and 6 to 12 inch depths in the unburned seeding plots. Some variations occur from year to year, but in the main the relations between the stations continue rather constant. The soil moisture on the northeast aspect and on the low flat, with

TABLE 12. SOIL MOISTURE IN PERCENTAGE OF DRY WEIGHT IN SEEDBEDS AT 1 TO 6 INCH DEPTH IN 1913

Surface	Flat		SW Slope		NE Slope	
	Average	Minima	Average	Minima	Average	Minima
Vegetation	19.7	9.6	16.5	2.1	40.1	21.9
Burned	18.4	6.9	16.7	2.8	45.2	11.8

TABLE 13. MEAN AND MINIMA OF SOIL MOISTURE IN PERCENTAGE OF DRY WEIGHT FOR AUGUST, 1914

Depth	Station 1 Flat		Station 2 SW Slope		Station 3 NE Slope		Station 4 Flat	
	Mean	Minima	Mean	Minima	Mean	Minima	Mean	Minima
Surface	7.0	2.1	7.7	0.5	43.6	0.7	19.1	0.4
1-6 inch	12.8	5.7	12.6	2.1	43.7	11.8	36.5	10.3
6-12 inch	13.4	5.0	13.2	2.6	43.9	11.9	39.3	10.6

TABLE 14. SOIL MOISTURE IN PERCENTAGE OF DRY WEIGHT IN LOCAL AND COMMON SOILS AT 1 TO 6 INCH DEPTHS FOR AUGUST, 1915

Soil type	Station 1 Flat		Station 2 SW Slope		Station 3 NE Slope		Station 3a NW Slope		Station 4 Low Flat	
	Ave.	Min.	Ave.	Min.	Ave.	Min.	Ave.	Min.	Ave.	Min.
Local soil	10.1	7.3	12.1	4.6	33.7	....	37.3	14.9	21.8	16.7
Common soil	9.2	6.3	8.6	3.4	19.2	19.2	30.5	12.5	15.3	13.8

western white pine and cedar-hemlock association, is always in excess of that on the other slopes. As the summer advances, white pine sites maintain high and safe levels, the steep northwest aspect becomes intermediate and the steep phase western yellow pine at 2a the driest. On the exposed western yellow pine site and on the flat the surface minima become surprisingly low. This brings about critical conditions in seed germination and seedling survival, but with small influence on the well established forest trees.

It was found that the moisture content at 6 to 12 inch depths for 1914, an average dry year, hovered around the minimum for a period of 42 days on the western yellow pine slopes and for a period of 25 days on the flat, but did not go below 20 percent on the white pine northeast aspect.

SEEDING TESTS

The results of the seeding tests are given in Table 15. In Fig. 12 are shown the distribution of seedlings in the quadrats in the presence of vegetation.

TABLE 15. GERMINATION, SURVIVAL, AND GROWTH OF SEEDLINGS, 1913-1917

Site	Location		Germination Percent		Percent survival to 1917	Height in 1917 in inches	Losses in 1913, Percent				
	Bed	Surface	1913	Total			Damping off	Rodents	Non-estab.	Cutworm	Unknown
					WESTERN WHITE PINE						
Flat....	E	Natural	7.0	10.5	7.2	6.5	66.6	—	—	11.1	22.3*
Flat....	E	Burned	3.2	12.8	90.6	6.9	53.9	—	—	38.5	7.6
SW....	C	Natural	1.2	9.1	0.0	—	50.0	13.6	—	22.6	13.6
SW....	C	Burned	0.7	6.9	0.0	—	72.7	—	—	—	27.3
NE....	A	Natural	11.4	12.8	82.9	4.3	30.3	—	3.0	16.7	50.0
NE....	A	Burned	10.9	13.8	84.6	4.6	56.3	—	6.3	12.5	25.0
					DOUGLAS FIR						
Flat....	E	Natural	15.9	17.9	80.0	5.7	52.0	0.0	8.7	0.0	39.3
Flat....	E	Burned	22.6	23.2	65.6	10.2	46.8	0.0	36.1	0.0	17.1
SW....	C	Natural	3.7	7.3	2.7	—**	73.6	0.0	0.0	11.7	14.7
SW....	C	Burned	4.3	7.5	2.7	—	74.4	2.3	0.0	4.6	18.7
NE....	A	Natural	0.5	5.1	25.9	6.0	77.5	0.0	6.5	6.5	9.5
NE....	A	Burned	15.0	15.6	79.5	5.5	40.5	0.0	9.5	0.0	50.0
					WESTERN HEMLOCK						
Flat....	E	Natural	1.0	1.0	0.0	—	26.1	0.0	0.0	0.0	73.9
Flat....	E	Burned	4.0	4.0	1.7	—	74.6	0.0	0.0	0.0	21.1
SW....	C	Natural	3.0	3.0	0.0	—	87.8	0.0	0.0	0.0	12.2
SW....	C	Burned	0.03	0.03	0.0	—	100.0	0.0	0.0	0.0	0.0
NE....	A	Natural	3.4	3.4	27.9	6.7	46.0	0.0	0.0	0.0	54.0
NE....	A	Burned	2.9	3.1	32.0	2.2	43.0	0.0	21.5	0.0	35.5
					WESTERN YELLOW PINE						
Flat....	E	Natural	17.6	21.6	87.5	8.8	35.6	0.0	10.8	10.8	42.8
Flat....	E	Burned	45.6	49.0	84.5	10.6	50.0	0.0	21.2	0.0	28.8
SW....	C	Natural	18.4	21.9	34.2	7.6	66.6	4.2	4.2	4.2	20.8
SW....	C	Burned	15.3	20.1	77.6	8.5	56.5	0.0	0.0	17.4	26.1
NE....	A	Natural	23.4	23.7	54.8	7.0	78.0	0.0	2.5	0.0	19.5
NE....	A	Burned	41.6	41.7	71.7	9.4	57.6	0.0	11.6	7.1	23.5
					WESTERN LARCH						
Flat....	E	Natural	2.5	2.8	17.2	2.6	66.6	0.0	0.0	2.1	31.3
Flat....	E	Burned	7.8	9.2	9.4	4.1	72.9	0.0	11.8	1.2	14.1
SW....	C	Natural	2.4	12.4	0.0	—	87.2	1.1	0.0	1.7	10.0
SW....	C	Burned	1.8	6.4	0.0	—	54.6	20.6	2.4	0.0	22.1
NE....	A	Natural	1.6	1.6	6.6	—	79.2	0.0	3.0	0.0	17.8
NE....	A	Burned	2.2	3.6	7.2	2.4	73.0	0.0	4.3	0.0	22.7
					WESTERN RED CEDAR						
Flat....	E	Natural	0.2	0.2	33.2	—	66.7	0.0	0.0	0.0	33.3
Flat....	E	Burned	0.2	0.2	10.0	—	42.8	0.0	0.0	0.0	57.2
SW....	C	Natural	0.1	0.1	0.0	—	50.0	0.0	0.0	0.0	50.0
SW....	C	Burned	0.02	0.02	0.0	—	0.0	0.0	0.0	0.0	—
NE....	A	Natural	0.2	0.2	22.2	2.0	43.0	0.0	0.0	0.0	57.0
NE....	A	Burned	0.4	0.4	29.0	4.2	33.3	0.0	0.0	11.0	55.7

*Percentages of total 1913 losses. **Losses subsequent to 1915.

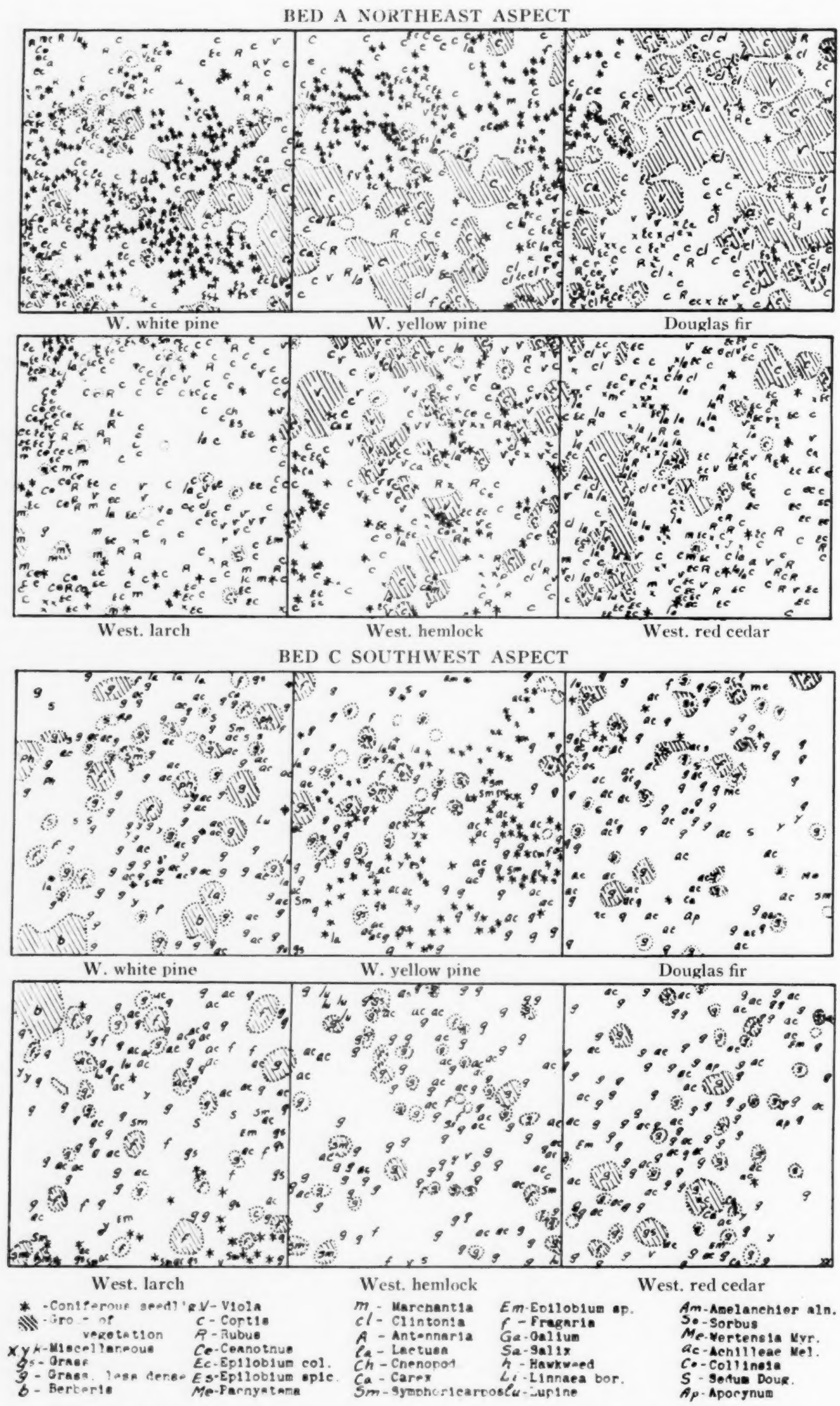


FIG. 12. Seeding quadrats on flat, southwest, and northeast slopes at Stations 1, 2, and 3.

The quadrats were made within the seedbeds with undisturbed vegetation and with cleared and burned surfaces. In the burned area liverworts, moss, and ground lichens appeared.

The quadrats were made to show the position of the seedlings, which are marked with asterisks, the type of vegetation on the various plots, and its relation to germination and survival. Hatched areas represent solid mats of vegetation, the individual plants being marked with a key letter. The density of the vegetative cover, therefore, may become a factor affecting the restocking, and since this matter leads us into an unexplored field, further discussion of this phase must be omitted.

Referring to Table 15, it is seen that western white pine germinated best on the northeast aspect in bed A; next best on the flat in bed E; and somewhat poorer on the southwest in bed C. There was generally better germination on the vegetation surfaces, especially during the first season. During the second season, however, many additional seedlings appeared, but more on the burned than on the unburned ground.

The fact that considerable seed of western white pine germinated during the second season after sowing, and that this germination was greater on the exposed southwest slope and flat, indicates that some of the seed remained viable and was better preserved under the drier conditions than in moister surroundings. The second-year seedlings were fully as vigorous as those of the first year.

The white pine survived better on the northeast slope and on the burned surface on the flat than elsewhere, with total failure on the southwest. The survival on the flat continued for a few years until competition eliminated most of the trees. At the end of 1917 the northeast aspect showed by far the best results. A slightly better height growth was observed on the flat than on the northeast slope. (See Fig. 13 for height and general development of the seedlings on the two kinds of surfaces.)

For the western yellow pine the results listed in Table 15 show a germination of 21.6 percent on the natural and 40.0 percent on the burned surface on the flat; 20.0 and 20.1 percent in the same order on the southwest slope; and 23.7 and 41.7 percent on the northeast aspect. From these results it is seen that, except for the exposed western yellow pine slope, the germination practically doubled on burned ground. Survival was good on all sites, but better in general on the burned surfaces than on the unburned; and height growth was much superior on the burned plots.

The second year's germination of western yellow pine increased the stand by 3 to 5 percent on the southwest aspect and on the flat, but not on the northeast. Since the 1913 season was very moist generally, the losses by damping-off were severe, especially on the northeast aspect and in the presence of vegetation.

Douglas fir germinated on the whole best on the flat and poorest on the southwest slope, the burned surfaces holding the lead on all three sites. The

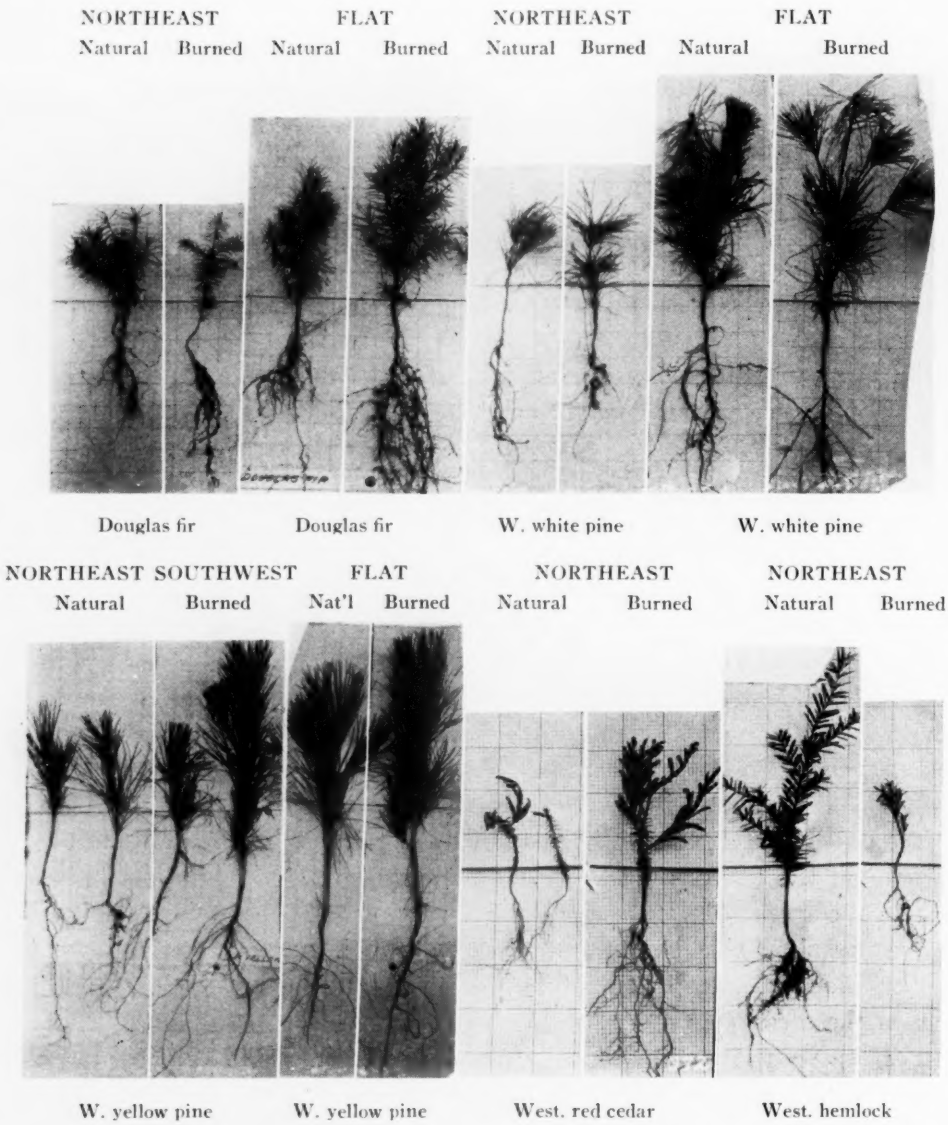


Fig. 13. Development of seedlings on burned and unburned surfaces at Stations 1, 2, 3, or flat, southwest, and northeast aspects.

second season's germination took place in all of the beds and added from 0.6 to 3.5 percent, being strongest in the presence of vegetation. Survival showed nothing on the southwest aspect in 1917, medium on the northeast aspect, and good on the flat; height growth was 10.7 inches on the burned surfaces, and only 5.7 inches in vegetation on the flat. For the northeast slope the height growth gave 6.0 inches in vegetation and 5.5 on burned surface (Table 15 and Fig. 13). Losses by damping-off were uniformly severe on all sites.

Germination of western larch showed best results on the burned surfaces, more particularly on the flat, and took the lead in the presence of vegetation

during the second season, with very good results on the southwest slope. Survival on the northeast and the flat continued good until the end of 1917, but was nil on the exposed southwest slope. None survived in the natural surface on the flat. Growth appeared more rapid on the burned surfaces, and losses from damping-off were severe on all sites during the first season.

The seed of western hemlock germinated very much better on the northeast and poorly on the southwest aspect, where it gave the better results on the unburned plot. In this respect we have a reversal from what took place on the flat, for in this location more seedlings appeared on the burned plot. Final survival can be credited only on the northeast location, where it was appreciably better on the natural than on the burned ground. The seedlings in the presence of vegetation grew to greater heights than those on the burned plot. The hemlock stand was greatly reduced by damping-off fungi, this loss being heavier on burned than on unburned surfaces. In this respect, this species differs from all others used in this experiment.

NATURAL SEEDING AND ESTABLISHMENT OF SEEDLINGS

It is true that conditions may exist where individual herbaceous and other plants would reduce the effect of climatic extremes and protect young trees. This seems to have benefited the larch and western red cedar. However, the keen competition for moisture and light which must be endured by the young trees growing in dense vegetative cover usually more than counteracts any advantages from protection afforded by that cover.

That the type of vegetation varies distinctly according to the site or exposure is sufficiently brought out by the lists of species given in Figure 12. On the northeast slope there occurs a larger proportion of the succulent plants, among which are Viola, Clintonia, Mertensia, and Rubus, and relatively few drought resisting varieties, such as Heuchera, lupine, Calamagrostis, Apocynum, and Sedum, which occur in greater abundance on the southwest exposure. The vegetation on the flat bears a closer resemblance to that on the northeast aspect and supports a great many additional plants of the genera Achillea, Fragaria, Carex, Berberis, and Pentstemon.

This subdominant surface cover of miscellaneous species moves in its own successional stages and cycles, which are little understood; and although this investigation did not include a quantitative study of the herbaceous cover, the writer recognizes its value and possibilities as an indicator of site characters and quality.

Within the altitudinal zone occupied by the western white pine, cedar, and hemlock, the western white pine is quick to reseed the terrain following single burns and destruction of the old forest. For this reason northern Idaho possesses many splendid stands of relatively pure western white pine. In a great many locations, such as small natural openings in the canopy, cedar and hemlock seed is naturally present along with the pine, both being more mesic and more tolerant of shade than the white pine; but their much slower

growth results in an understory. As the overstory of pine eventually decays, the cedar and hemlock become dominant.

If the western larch, which has temperature and moisture requirements quite similar to white pine, seeds in together with the pine, its rapid height growth enables it to keep ahead of all other species. Its deeper root system gives it an added advantage on sandy benches. It therefore remains in the forest for several hundred years until the climax species succeed the white pine.

Successful establishment and growth of western yellow pine seedlings requires a mean seasonal soil temperature between 60 and 70° F., and from 50 to 100 percent of light in summer. It will tolerate lower soil moisture than any of the other species tried.

Although individual trees of western yellow pine will be found within the young stand on white pine sites, their form and development is much inferior, and their growth slow as a result of competition with the white pine for moisture and light. They are eventually overtopped and suppressed, disappearing from the stand at a relatively early age.

Natural regeneration of Douglas fir succeeds well on both natural and slopes and very cold flats; and it appears that the slight protection offered bare surfaces on north slopes and flats, but is uncertain on the very warm by shrubbery from the drying influence of wind and sun in midsummer and by the accumulation of leaf litter from shrubbery, which improves the moisture capacity of the soil, are here very beneficial to the establishment of Douglas fir. This intermediate species will germinate and become established in western yellow pine stands only with this added protection, and in white pine and cedar stands, if competition is greatly reduced.

For successful establishment of western larch there must be assured sufficient soil moisture in the upper layers of soil 1 to 6 inches and 6 to 12 inches throughout the entire first growing season. This means at least 20 percent of moisture in the soil above the 10-inch level. Fully 75 percent of sunlight is also needed, and unobstructed sunlight is not harmful.

Larch and western yellow pine seldom compete on the same terrain in northern Idaho. They are both quite intolerant of shade, but the larch grows under conditions of lower temperature and higher soil moisture than western yellow pine, and it belongs to a higher zone. If they germinate side by side, the lack of soil moisture becomes the determining factor in favor of the pine; and if soil moisture is sufficient, the larch speedily outgrows the yellow pine.

Competition between the larch and the Douglas fir is chiefly for soil moisture in that these two species grow equally well under identical atmospheric conditions. The larch seedlings cannot survive where the soil moisture becomes low during the middle or latter part of the summer. This leaves the Douglas fir in possession of the steeper gradients similar to the northwest aspect where Station 3a was situated. The larch holds sway on benches and

lower northerly slopes; here it finds favorable conditions for rapid development, often becoming dominant.

Establishment of western hemlock requires soil moisture not below 20 percent and at least 20 percent of full sunlight. These conditions are met on better soil in the breaks in the virgin timber on flats and northerly slopes. The seedlings are rapidly eliminated from bare or exposed surfaces because of a dry soil and lack of protection from heat or too rapid transpiration. Hemlock seedlings have shallow roots. They thrive in moist, sheltered places and on soils with much organic material, especially in decaying wood. They frequently present considerable competition to seedlings of western white pine.

Cedar requires constant soil moisture not below 12 percent in August, such as is found on the north aspects and loamy flats. It will not withstand full sunlight. The failure of western red cedar and western hemlock on the southwest slope is ascribed chiefly to the more exacting conditions arising from the greater wind movement, lower humidity, warmer soil, and the less stable soil-moisture content. Requirements of hemlock and western red cedar are nearly identical; but unlike hemlock, cedar made noticeably better growth on the burned and denuded surface, and appears less selective than hemlock for organic material and decaying wood.

PLANTING TESTS

Results obtained in the planting experiments are given in order for series A, B, C, and D. These tests have been described in the section on methods. Data on survival and growth are included in Tables 16 and 17, and the curves for survival and growth of series A to C, in Figures 14 and 15.

In series A (Figures 14*A* and 14*B*) the western yellow pine proved uniformly better in survival and growth on the flat than on the southwest slope. The height growth was 57 inches at the end of 1921 on the flat and only 15 inches on the slope. It is true that there has been more grass and shrub competition on the slope than on the flat, but even in the absence of competition the trees on the exposed slope measured at the end of 1921 only one-half the height of similar trees growing on the flat. On both sites the transplant stock showed superiority over the seedlings.

In series B (Fig. 14*C*) western yellow pine substantiated in a very clear manner the results obtained in the previous test in showing 56 percent survival and 29.5 inches on the flat compared with 44.0 percent survival and only 15.8 inches in height on the southwest aspect. A proportionately greater mortality occurred among the smaller classes on the southwest aspect than on the flat. This was in all probability caused by the lower moisture content in the soil in the upper layers on the slope; greater air movement, and evaporation.

Since the flat is underlaid by a porous material to considerable depth and the southwest slope rests on solid rock, the plants on the two sites in series A and B were subjected to somewhat unequal soil-moisture condition.

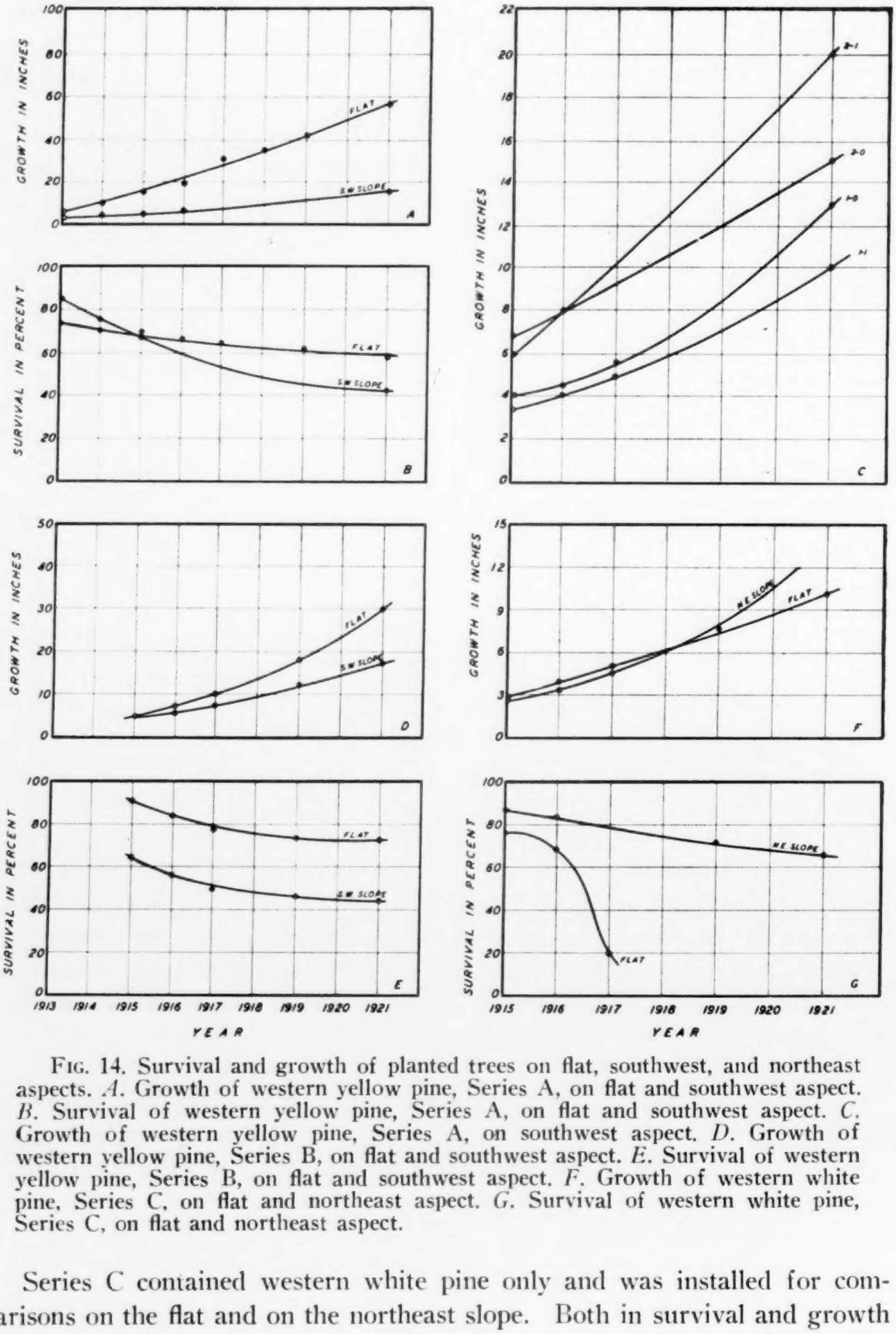
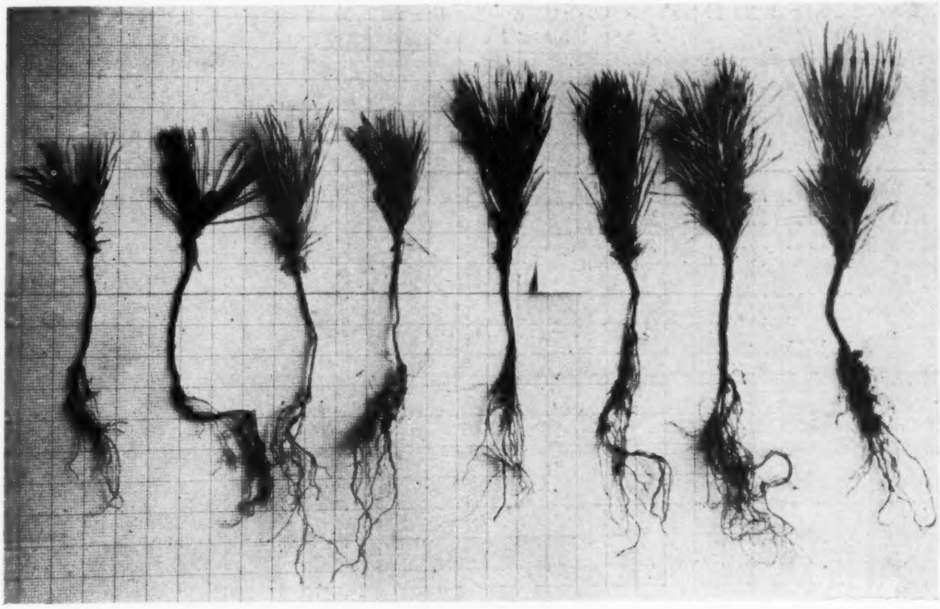


Fig. 14. Survival and growth of planted trees on flat, southwest, and northeast aspects. *A*. Growth of western yellow pine, Series A, on flat and southwest aspect. *B*. Survival of western yellow pine, Series A, on flat and southwest aspect. *C*. Growth of western yellow pine, Series A, on southwest aspect. *D*. Growth of western yellow pine, Series B, on flat and southwest aspect. *E*. Survival of western yellow pine, Series B, on flat and southwest aspect. *F*. Growth of western white pine, Series C, on flat and northeast aspect. *G*. Survival of western white pine, Series C, on flat and northeast aspect.

Series C contained western white pine only and was installed for comparisons on the flat and on the northeast slope. Both in survival and growth this series (Fig. 14*D*) points unmistakably to the northeast aspect as the more suitable site for western white pine, with survival of 78 percent for 1-2 planting stock and 66 percent for 2-0. The flat proved to be a very



A

B

FIG. 15. *A*. Representative stock of western yellow pine planted spring 1914 on the flat and southwest slope. *B*. The same stock as photographed in 1932.

unfavorable environment for western white pine, very few of which remained until 1921. The 1-2 transplants survived and grew better than the 2-0 stock.

On the steep southerly sites in series D (Table 16) 1-2 transplants of western yellow pine showed higher survival than 3-0 stock. The survival of

TABLE 16. SERIES D; PLANTED STOCK OF 3-0 AND 1-2 WESTERN YELLOW PINE ON STEEP PHASE SOUTHERLY ASPECTS

Location	Station	Class	Survival in Percent		Height in Inches	
			1915	1921	1915	1921
SW Slope	2a	3-0	35	22	9.1	21
S Slope	2b	3-0	45	24	10.0	23
SE Slope	2c	3-0	26	12	11.0	24
SW Slope	2a	1-2	61	27	6.7	18
S Slope	2b	1-2	65	26	7.7	16
SE Slope	2c	1-2	49	14	8.6	21

TABLE 17. GROWTH OF THE DOMINANT TREES IN THE PLANTATIONS TO THE END OF 1932

Series	Location	Species	Average height in inches	Number of trees	Total age; years	Average height growth in inches
A	Flat	Western yellow pine	182.4	51	20	9.1
A	SW Slope	Western yellow pine	80.1	21	20	4.1
B	Flat	Western yellow pine	114.2	100	18	6.3
B	SW Slope	Western yellow pine	88.2	36	18	4.9
C	Flat	Western white pine	75.5	12	17	4.4
C	NE Slope	Western white pine	85.6	100	17	5.0
D	SW Slope	Western yellow pine	74.4	12	17	4.3

3-0 plants was 22 percent on the south and 12 percent on the southeast face of the hill. For 1-2 stock it was 27 percent and 14 percent in the order given, the south face falling close to the west with 26 percent survival. The results are clear-cut in that these critical sites, as indicated by the soil tests and field soil-moisture tests previously discussed, were the determining factor in low survival and rather slow growth. In the matter of relative height growth no constant or significant differences are evident. It appears from this series on the three exposures that the southeast is the most precarious or exacting. The underlying rock may have some influence on the soil moisture relations.

The measurements obtained during the autumn of 1932 of series A, B, C, and D were made on the dominant trees regardless of original size classes. In several of the plantations 50 or more dominant trees were not available.

Records from the plantation measurements in the autumn of 1932, which are summarized in Table 17, repeat and confirm the earlier results with western yellow pine in showing better growth for series A and B on the flat than on the southwest slope. On the flat, plants of series A averaged 9.1 inches in annual height growth from the time of planting, and those on the southwest only 4.0 inches; and plants of series B averaged 6.3 and 4.9 inches. In series C, with western white pine, those on the northeast aspect show

an average height growth of 5.0 inches and those on the flat 4.4 inches over a period of 18 years. Of the white pines set out on the flat, only 12 survived out of 100. In series D, western yellow pine planted on the steep phase yellow pine site at 2a, the few surviving plants averaged 4.3 inches in height growth from 1915 until the end of the growing season in 1932.

Summarizing the results from the planting tests it appears that the results have confirmed, in a large measure, the natural selectivity of the species for given sites expressed earlier in the seeding tests; in that western white pine survives and grows better on soils with more nutrients and improved moisture-holding capacity, and that western yellow pine takes the lead on warm, dry sites with porous and somewhat impoverished soils. These planting tests have gone a step farther than the seeding experiments, since they show a definite correlation of survival and growth of western yellow pine with soil quality and nutrients; a superior development under the most favorable edaphic conditions on the flat, intermediate on the southwest slope at Station 2, and poorest on the steep phase situation at Station 2a.

It appears that the results obtained by the seeding tests and corroborated by the planting experiments have told the story better than any other set of data. Reduction in evaporation, as effected by decreased temperature and wind and by increased humidity, resulted in higher soil moisture, denser vegetation, more abundant organic material and nutrients, which in turn favored establishment and development of mesic species, especially western white pine, on protected sites, and caused its elimination from exposed aspects. In a similar way we may trace the selection by other species of their proper habitat within the succession. This selection of the most suitable location is accomplished during the very first and second years in the life of the trees. However, on intermediate sites, the more mesic species may invade and remain semi-suppressed for a long period of time and begin more active growth leading to dominance upon the elimination of more xeric species from the stand.

The order of secondary plant succession in northern Idaho, as determined by this field study of habitat requirements of the species, is from western yellow pine, through western white pine to the red cedar-hemlock climax.

Western larch has a place in the western yellow pine stage under more favorable moisture conditions, and grand firs occurs in the Douglas fir stage under the same conditions.

SUMMARY AND CONCLUSIONS

A study was initiated in 1912 at the Priest River Forest Experiment Station in northern Idaho, seeking to determine and evaluate site factors governing the re-establishment of temporary forest types of the secondary forest succession following forest fires, logging or other denudation.

Subsequent to general forest fires, which occur periodically in this region and which are very destructive, reseeding and natural return of a forest takes place by stages passing from the intolerant and xerophytic trees to the more permanent, tolerant, and moisture-demanding species.

The investigation embraced a study of the climatic and edaphic factors and an analysis of the soil with a view to evaluating the mechanical, physical, and chemical properties. Responses of artificially-sown native seedlings and planted trees formed a part of this study.

Several well-equipped weather stations were therefore located on a flat bench in larch-Douglas fir forest, on a southwest western yellow pine slope and on a northeast aspect within the western white pine type. Other secondary stations were chosen and the records for the main stations continued over a period of 5 years.

The results obtained from this study are briefly summarized as follows: air temperature relations show higher daily and seasonal maxima on the southwest aspect with a longer duration of temperatures favorable for growth than at the other points. Conditions were almost as favorable at the station on the flat, but the northeast aspect shows the least extreme in the maxima. The minima of the air temperatures were lowest on the flat both winter and summer and highest on the northeast slope. From these relations it follows that the greater ranges and the danger from frost is more acute on the flat than at the other points.

Soil temperatures reflect and follow the trend of the air temperatures, but diverge far more at the surfaces and in the upper soil stratum than at the lower levels. The absolute maximum of surface readings were, on the southwest aspect, 125° F., on the flat, 100°, and on the northeast, 95° F.

The southwest aspect which supports western yellow pine is characterized by a shallower snow cover, which is also of shorter duration than on the other sites. This site is also favored above the others by higher maximum air temperature in summer and a longer period of growing temperatures. The soil moisture reaches more critical minima and remains at dangerously low points for extended periods in summer, and wind movement and evaporation are more pronounced than elsewhere. The opposite is true for the northeast aspect, while the flat falls between these two.

The soils on the northeast slope and at situations where the mesic species grow contain a greater clay and silt fraction and higher capillary and other moisture-retaining qualities than those occupied by the xerophytic western yellow pine. These "mesic" soils show also a higher wilting coefficient and contain larger percentages of nitrogen, organic material, and phosphorus than the soils of the exposed aspects. In all of these relations the larch-Douglas fir site appears to be intermediate.

Soils of the more sandy flats which become occupied with larch and Douglas firs are ordinarily not sufficiently improved in physical properties

to favor the growth of western white pine, cedar, and hemlock. These areas will therefore remain in larch and Douglas fir indefinitely, while the more favorable soils are reclaimed by species of greater tolerance and moisture requirements.

Seedlings which were raised from seed on the different sites expressed, by their germination during the first two seasons and by their survival and height growth to the end of the fifth year, a conformity to the already existing forest trees which had seeded in after the fires of 60 years ago, in that the white pine survived only on the northeast aspect, and the western yellow pine was practically the only species out of six which survived on the exposed southwest slope.

This same tendency was found to hold true also in the plantations of western yellow pine and western white pine; the former was not planted on the northeast aspect, but the white pine survived and grew far better on the northeast slope than elsewhere, it being a total failure on the southwest site and gave very poor results on the flat.

These results demonstrate an early selectivity of the native species for their more suitable environmental conditions which is expressed primarily through their survival and later development rather than their germination, for germination of the western white and western yellow pines may take place on all of the aspects and on different surfaces. The failure of the mesic species to survive the peak of the hot and dry first summer on exposed sites and the elimination of xerophytic species by fungus growth, lack of light, and competition during the early part of their existence bring about the distribution which we have endeavored to explain.

It appears that the edaphic conditions to a large extent control and determine the order or stages in the progression of the temporary types, especially through factors of soil, temperature, soil moisture, and water-holding capacity. But these characters are to a great extent the products of climatic factors, which vary for both the exposed and for the protected aspects. On the flats and benches, however, the type of forest which forms a part of the succession depends in large measure upon the condition of the soil and its ability to hold moisture throughout the critical part of the summer.

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THE DISTRIBUTION OF SOME CLADOCERA AND FREE-LIVING COPEPODA IN BRITISH COLUMBIA

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CONTENTS

THE DISTRIBUTION OF SOME CLADOCERA AND FREE-LIVING COPEPODA IN BRITISH COLUMBIA

INTRODUCTION

In the following paper data are given on the occurrences of some Cladocera and free-living Copepoda in lakes and pools in certain portions of the Province of British Columbia and some theories are advanced in an attempt to explain the present distribution of these organisms in this area.

In the past many attempts were made to explain the occurrence of animals and plants in certain parts of the world but the close affinity between the present distribution of life and the past history both of living organisms and of the earth was not recognized until quite recently. This concept of zoogeography is expressed by Ortmann (1902), Scharff (1911) and others, who use their data to support the theory of the existence of land connections between continents or to give evidence regarding the date, duration and effect of the Pleistocene ice age. However, it seems advisable to try to determine some of the factors controlling distribution of organisms in the present and then to consider possible factors affecting distribution in the past. Such a procedure is attempted in connection with the Cladocera and Copepoda of British Columbia.

In considering the distribution of plants and animals in a broad perspective the works of Wallace (1876, 1892), Heilprin (1887) and Willis (1922) are of great value. Information regarding the distribution of freshwater Entomostraca in Europe and Asia is made available through the works of De Guerne and Richard (1889), Tollinger (1911), Sars (1900, 1903), Gurney (1931-33), Wesenberg-Lund (1908), Schmeil (1892), Smirnov (1930), Rylov (1922, 1930), Ekman (1905) and others. In North America our knowledge of the distribution of these forms is comparatively meager since large areas, particularly in the northern part of Canada, are yet unexplored. Most of the records of distribution in this continent are in the publications of Schacht (1897), Marsh (1907, 1918, 1920, 1929), Willey (1923, 1927, 1931), Forbes (1897), Wilson (1932), Dodds (1919, 1920, 1924), Birge (1918), Herrick and Turner (1895), and others.

As a result of the fragmentary nature of our present knowledge of these organisms the distribution of some species appears to be exceedingly discontinuous with the result that many problems exist regarding the origin and relationships of these isolated groups. Contributions, such as the present study, may serve to fill in some of the extensive gaps which still exist by providing records from hitherto unknown localities and analyses of the accumulated data may contribute to a more complete understanding of the factors involved in controlling distribution.

MATERIALS AND METHODS

SOURCE OF MATERIAL

The material used in the investigation upon which the present paper is based, has been taken, of necessity, from many sources and by different means. A few of the records have been taken directly from previous publications such as those of Foerster (1925), Thacker (1923), Rawson (1934) and Wailes (1930). Many records have been obtained from samples collected during investigations of various lakes such as Okanagan, Cowichan, Shawnigan and others, but by far the greatest number are from samples collected by private individuals and by fishery officers in various parts of the Province. The following table shows the areas covered by collections from all sources and the number of lakes or other bodies of water in each area from which collections have been made or from which records have been obtained.

	Number of lakes
Coastal belt (Graham, Vancouver and Salt Spring island and lower mainland east to Coast range)	79
South Dry belt (Okanagan, Nicola and Kamloops)	77
North Dry belt (Cariboo, Quesnel, Burns and Babine regions)	51
Interior Wet belt (Kootenay district)	14
Rocky Mountain belt (Cranbrook and Invermere)	8
Miscellaneous areas: Dease river (Fort McDame)	3
Portland canal (Hyder, Alaska)	1
Total	233

The relative sizes of the areas covered and the geographic relationships are shown in Figure 1.

EQUIPMENT USED

In making the first collections a standard-sized net of the Wisconsin type as modified by Rawson (1934) was used, but this was later replaced by a simpler net of a smaller size which proved satisfactory. The net adopted was made of factory cotton or, in some cases, bolting silk and factory cotton attached to a metal ring having an outside diameter of six inches, the whole forming a cone about ten inches in length. A four drachm glass vial tied at the apex of the cone formed a convenient receiver for the catch. A piece of strong twine attached to the ring at three equidistant points provided a point of attachment for the means of towing the net through the water.

A net of this small size has several advantages: it is simply and cheaply constructed, it is easily carried or sent through the mail and the samples collected by it, being in small vials, occupy little space and are easily transported.

RELIABILITY OF SAMPLES

Since the nature of a plankton community depends upon several factors such as physical, chemical and biological conditions within the lake and cli-

Fig. 1. Map of British Columbia showing chief river systems and areas (cross-hatched) from which samples have been obtained.

matic conditions outside the lake its composition is in a constant state of change, particularly with respect to numbers, with the result that it is not possible to make an accurate numerical analysis of the population from one or two samples. However, it has been found from a series of samplings extending over several years that the crustacean component of a plankton community remains relatively unchanged as to species, some forms disappearing and reappearing at regular intervals according to the season but the majority persisting year after year. Therefore, since the present study is concerned with the occurrence of the various species and not with their relative numbers the records obtained from single samples have a value as great as those from complete series taken throughout the year. It must be remembered, however,

that the absence of certain species from any sample cannot be accepted as evidence that the species is not present in the lake, since some forms, particularly those usually associated with the bottom or with water plants, are taken only occasionally in open water while others may be temporarily dormant.

ACKNOWLEDGMENTS

During the course of the present study the co-operation of many persons has been received. The writer wishes to express his thanks to the following: Dr. W. A. Clemens of the Pacific Biological Station, Nanaimo, who pointed out the possibilities of the investigation and made the undertaking possible; Dr. C. McLean Fraser of the Department of Zoology, University of British Columbia, who provided laboratory facilities; Professor Trevor Kincaid of the Department of Zoology, University of Washington, who identified many specimens, supplied others for comparison and provided information regarding distribution in the State of Washington; Prof. W. J. K. Harkness of the Department of Biology, University of Toronto, for supervision and guidance; Prof. J. R. Dymond, Director of the Royal Ontario Museum of Zoology, for assistance in preparation of the manuscript; Dr. R. E. Coker of the Department of Zoology, University of North Carolina, for identifications of some of the Harpacticoids; Dr. D. S. Rawson of the Department of Zoology, University of Saskatchewan, for use of unpublished reports and for contributing plankton samples; Mr. G. Morley Neal of the Department of Biology, University of Toronto, for extensive collections from Kamloops and Okanagan regions and for use of unpublished data.

The writer is also indebted to the following people who have assisted both in the collection of material and in the supplying of data. The names in parentheses refer to localities in which collections were made: Mr. W. M. Ferrier (Prince George), Mr. W. P. Forsythe (Kennedy lake), Mr. F. J. Winlow (Squamish), Mr. F. A. Tingley (Blue lake, Canim lake), Mr. J. E. Kew (Quesnel district), Mr. G. N. Gartrell (Okanagan region), Mr. F. Warne (Meziadin lake), Mr. C. H. Robinson (Kootenay district), Dr. W. A. Clemens (Forbidden Plateau region), Dr. A. L. Pritchard (Graham island), Dr. G. Hanson (Dease river district), Dr. I. McTaggart Cowan (Cariboo), Dr. D. McCaffrey (Princeton), Prof. G. J. Spencer (Chilcotin), Miss E. M. Halley (Salt Spring island), Miss Delma Brown (Hyder, Alaska), Mr. David Munro (Cariboo district), Mr. I. E. Cornwall (Shawnigan lake), Mr. J. B. Tighe (Sooke lake), Mr. S. Kilvington (Alberni region), Mr. R. L. Haig-Brown (Buttle lake region), Mr. J. Kendall (Kamloops region), Mr. J. H. Barclay (Aleza lake region), Mr. G. P. Holland (Coastal region).

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Scholarship, authorized by the Board of Governors, University of British Columbia, to be used for the completion of the investigation was received during 1936-37.

GEOGRAPHY OF BRITISH COLUMBIA

GEOGRAPHICAL POSITION

The Province of British Columbia is bounded on the north by the parallel of 60° latitude and on the south by the parallel of 49° latitude as far as the Strait of Georgia, and includes the whole of Vancouver island. On the east it is bounded by the summits of the Rocky Mountain chain from 49° to about 54°, thence up the meridian of 120° west longitude to the northern boundary. On the west the Province is bounded by the Pacific, north to Portland canal; thence the western boundary is the narrow strip of the Alaskan coast known as the "panhandle," as delimited by the 1903 London award. Its total area is 355,855 square miles.

GENERAL DESCRIPTION

British Columbia has been described as a "sea of mountains." The main structural features have a general north-west and south-east trend, in some instances extending the entire length of the Province, and in others for only a portion as illustrated by the physiographic map (Fig. 2).

The Rocky Mountains which are the dominant features of the physiography and which form part of the inter-provincial boundary on the east, rise to a general level of 8000 feet with several peaks reaching a height of over 13,000 feet above sea level. It forms a natural barrier to the spreading of animals and plants in the southern half of the Province, but towards the north, in the Peace river area, the range is broken through at several points by elevated plateaus extending westward from the Great Plains region of the prairie.

The Interior Plateau, sometimes considered as being composed of a number of small plateaus, stretches north-west and south-east for about 500 miles. The area as a whole rises in elevation toward the north with the result that the general level which is about 1000 feet in the lower Okanagan valley is increased to 1200 feet in the Kamloops region and to 2000 feet near Prince George. Most of the lakes west of this latter point lie at an elevation between 2100 feet (Fraser lake) and 2400 feet (Francois lake). Lakes of the Cariboo district, south-east of the same point, lie at an average elevation of about 3400 feet above sea level.

HYDROGRAPHY

The most important lakes are Babine, Stuart, Francois, Takla, Shuswap, Okanagan, Arrow and Kootenay. These, together with the remaining lakes, cover a total area of 1,560,830 acres or 2439 square miles.

The most northern part of the Province is drained by four main rivers, the Dease, the Peace, the Stikine and the Nass. Southward the most important river is the Skeena which is about 300 miles in length and drains the Babine and Morice lake districts. Two river systems only call for notice in the southern half of the Province, the Columbia occupying the south-eastern portion and the Fraser occupying nearly all the remainder (Fig. 1).

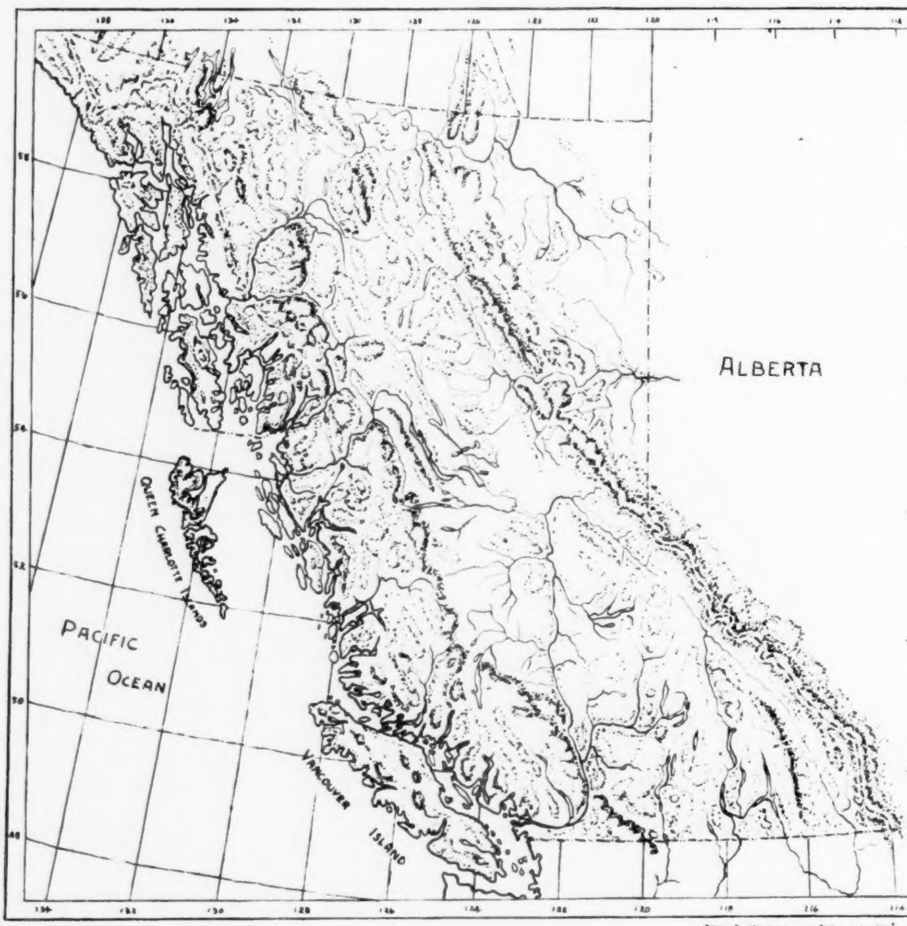

FIG. 2. Physiographic map of the Province of British Columbia.

GEOLOGICAL HISTORY

It is generally accepted that during portions of the Pleistocene period an extensive ice-sheet covered all the area which is now the Province of British Columbia. This expanse of ice, known as the Cordilleran sheet, originated in the Rocky Mountains somewhere between the 55th and 54th parallels of north latitude and spreading northward, southward and westward filled the coastal straits and covered most of the adjacent islands, the Queen Charlotte islands being an exception. It also spread eastward through the mountain passes to meet the advancing edge of the Keewatin ice-sheet which had its

center near Hudson Bay. Thus, the territory west of the Rockies, extending from parts of Alaska to a southern limit south of the 49th parallel of latitude was covered by an ice-sheet which may have attained a maximum thickness of 7000 feet in some places (Dawson 1893).

It is generally believed that practically all life in the glaciated area must have disappeared through destruction or migration (Coleman 1929, Wright 1911) but a few maintain that this is not necessarily true as certainly some mountain tops ("Nunataks") remained unaffected (Fernald 1925). However, large unglaciated areas existed to the north and to the south of this ice-sheet, forming havens to which animals may have retreated and in which many species of animals and plants undoubtedly maintained an existence. Evidence shows that the greater part of Alaska remained untouched by ice and, in fact, it is believed by some writers (Scharff 1911) that an almost tropical climate prevailed in this territory during the Glacial Period. It is also certain that most of the area now forming the United States was comparatively unaffected and supported a flourishing fauna. Thus, following the retreat of the ice an invasion of living organisms could take place mainly from two directions, from the south and from the north.

The effects of the Glacial Period upon the physiography of British Columbia are everywhere evident, particularly in extensive deposits of glacial till and scooped-out valleys. Drainage systems have also undergone changes in the past as made evident by the presence of old lake levels in many areas such as the Okanagan valley. The whole of the Province has suffered changes from the complete glaciation with the result that the history of its present-day flora and fauna dates back only as far as the final retreat of the ice which took place possibly about 8,000 to 10,000 years ago (Wright 1911).

CLIMATE OF BRITISH COLUMBIA

Owing to its geographic position and physiographic complexities the climate of British Columbia presents all the conditions met with in European countries lying within the temperate zone (Stanford's Comp. Geog. and Travel 1915). The series of parallel high mountain barriers alternating with areas of lesser altitude, all situated at right angles to the general direction of the westerly moisture-bearing winds, results in a corresponding series of longitudinal belts of climate, which show great differences in mean temperature and precipitation.

CLIMATIC BELTS

The *Coastal belt* comprises all the region west of the axis of the Coast mountains. The main characteristics are high precipitation and comparatively mild temperatures. The difference between average mean temperature of winter and of summer is not great. As an illustration of this the monthly averages of the normal daily maximum and minimum temperatures are given in graph form in Figure 3 for two widely separated points, Massett on Graham

island (Queen Charlotte islands) and Victoria on Vancouver island, which have climates fairly typical of the belt as a whole. It will be seen that the average maximum temperatures for both regions show a very narrow range and do not fall below 30°F. at any time as a result of the tempering effect of the adjacent ocean. The rainfall, however, varies from about 30 inches per year around Victoria to about 250 inches in certain small areas, depending

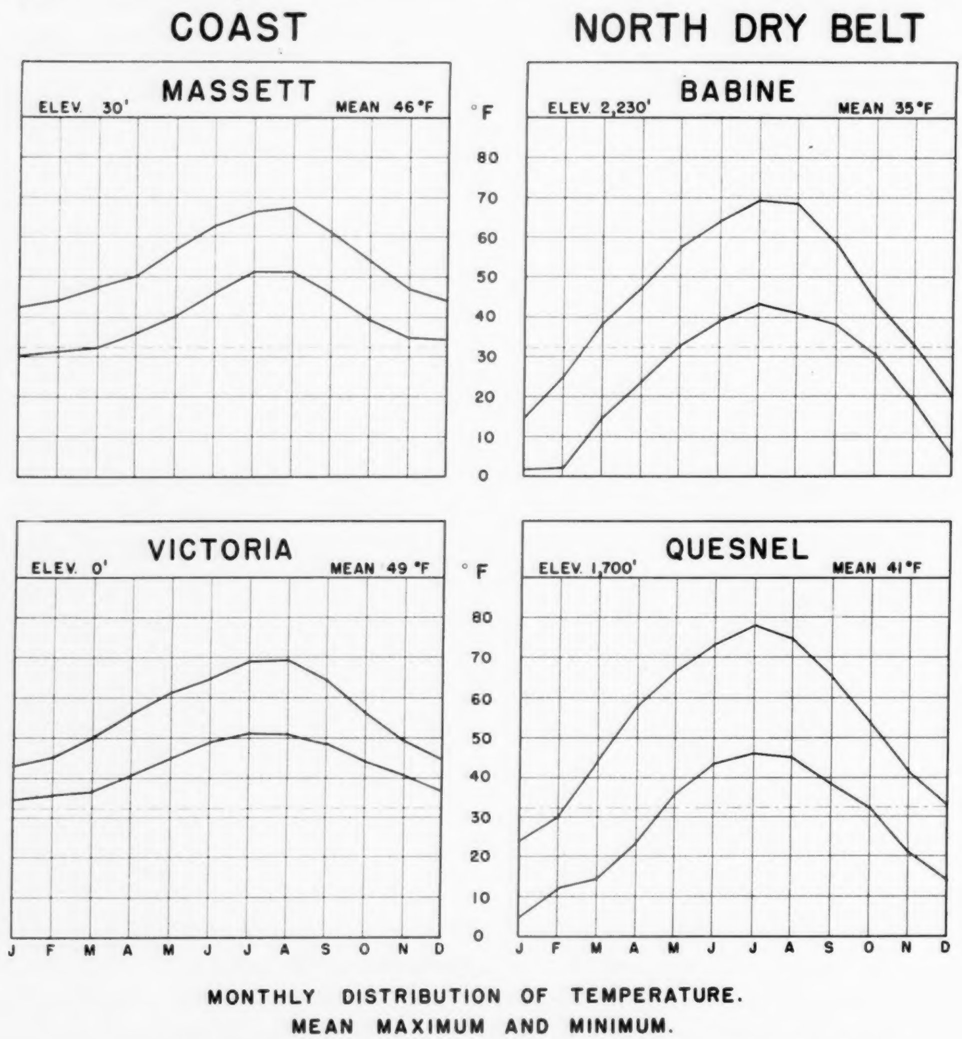

FIG. 3. Air temperature conditions in Coastal belt and in North Dry belt.

upon the position of minor mountain ranges. The total precipitation and its monthly distribution in the above two localities together with that of Nanaimo and Vancouver are given in Figure 5. The white areas indicate the amount of precipitation due to snowfall and the figures to left and right of the locality name refer to elevation and total precipitation respectively.

Contrasted with the Coastal belt, the *Dry belt* of the interior is characterized by greater extremes in temperature and much lower precipitation.

Reference to Figure 4 which shows maximum and minimum temperature for Kamloops and Kelowna situated in the southern part of the Dry belt will show that a much greater range of temperature prevails than in districts of the same latitude in the Coastal belt. Records from stations in the northern portion, such as Babine lake and Quesnel (Fig. 3) show similar extremes of tem-

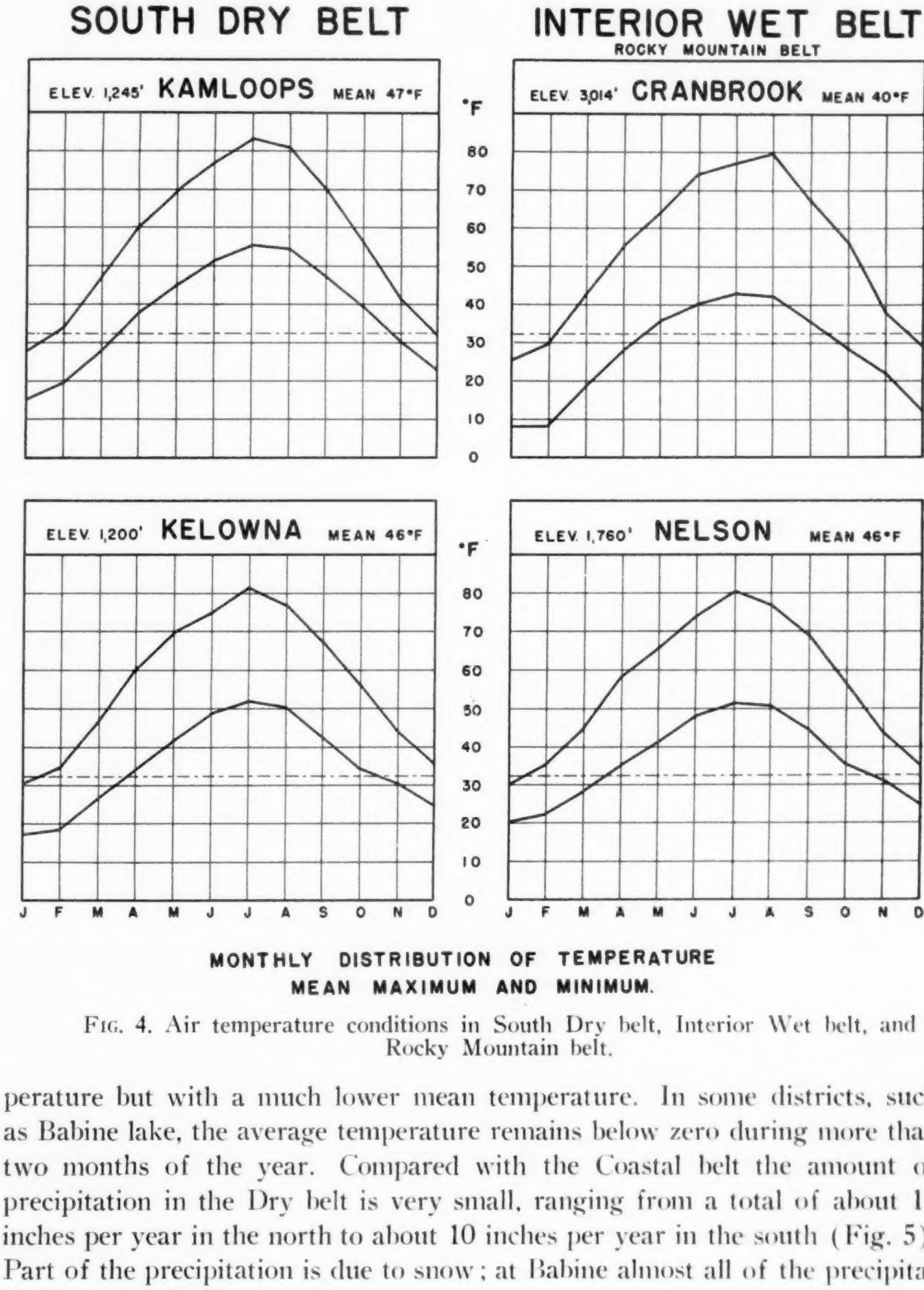

FIG. 4. Air temperature conditions in South Dry belt, Interior Wet belt, and Rocky Mountain belt.

perature but with a much lower mean temperature. In some districts, such as Babine lake, the average temperature remains below zero during more than two months of the year. Compared with the Coastal belt the amount of precipitation in the Dry belt is very small, ranging from a total of about 19 inches per year in the north to about 10 inches per year in the south (Fig. 5). Part of the precipitation is due to snow; at Babine almost all of the precipitation in the winter is in the form of snow.

East of the interior plateau is a secondary moist belt, usually known as the *Interior Wet belt* in which the general average precipitation is well over 30 inches and, in some cases, is as high as 60 inches per year. The mountainous valleys tributary to the main trenches have a higher precipitation than

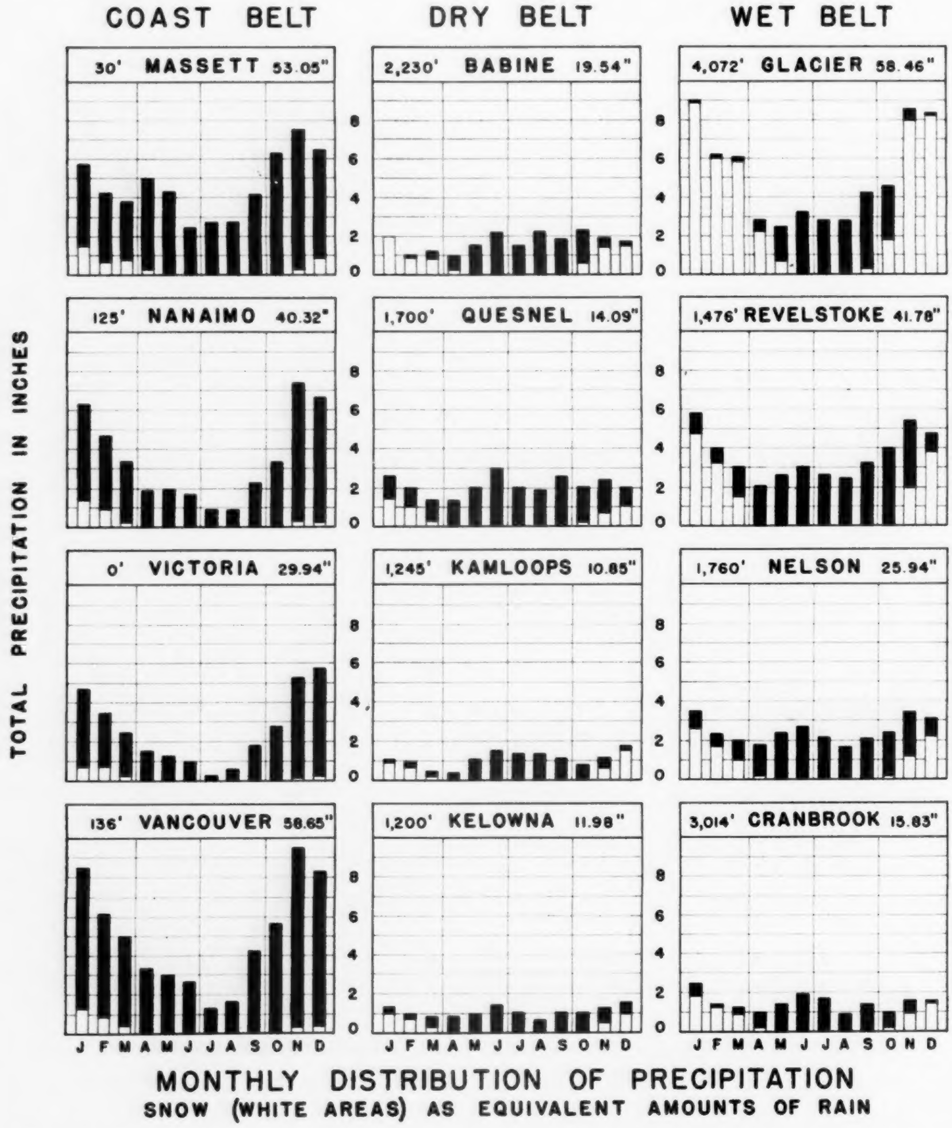

FIG. 5. Precipitation in Coastal belt, Dry belt (North and South), Interior Wet belt, and Rocky Mountain belt (Cranbrook).

the trenches themselves and a larger portion of this precipitation is in the form of snow. Thus Revelstoke (elev. 1497′) has a precipitation of 42 inches, one third of which is in the form of snow, while Glacier (elev. 4094′) has an annual precipitation of 58 inches, nearly two thirds of which is in the form of snow, as shown in Figure 5. Stations situated in the valleys of the southern

portion of the Interior Wet belt have a mean annual temperature of 44°F., with a mean winter average of 27°F. and a summer average of 61°F. Contrasted with the temperature conditions of the southern portion of the Dry belt (e.g. Kelowna) the summers of the Interior Wet belt are cooler, the winters slightly warmer, and the extremes not very far apart. Average maximum and minimum temperatures for Nelson in the Kootenay district, are shown for comparison in Figure 4.

Meteorological data for Cranbrook are also shown in Figures 4 and 5. Since this station lies west of the Selkirk range at an altitude of 3014 feet it is taken as typical of the southern portion of the *Rocky Mountain belt*. Here, the precipitation is again small, being about 16 inches per year, one quarter of which is due to snow. In general the temperature conditions are more severe than in other belts in the same latitude; during a period of more than a month the average maximum temperature does not rise above freezing (Fig. 4).

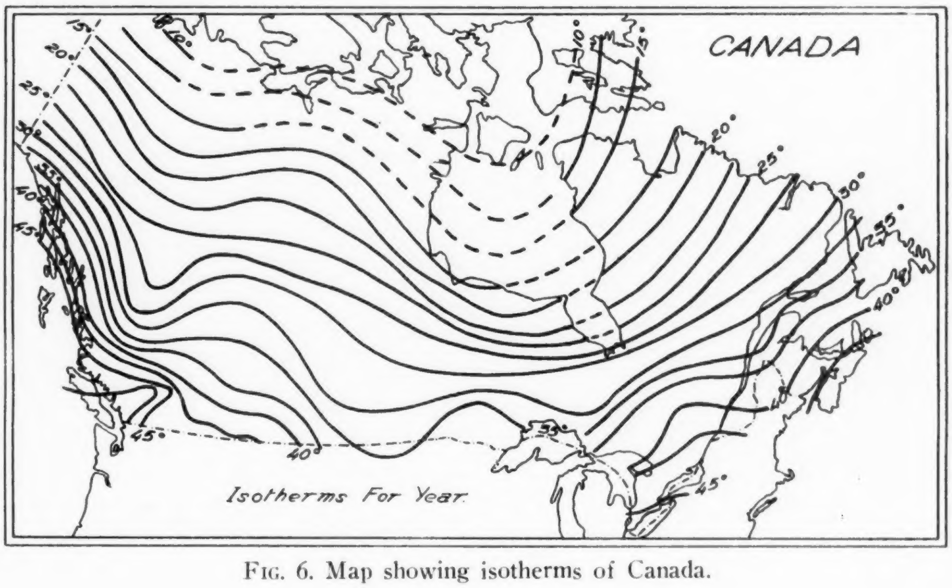

FIG. 6. Map showing isotherms of Canada.

ISOTHERMAL REGIONS

It has been shown that the climate of the southern portion of British Columbia can be divided into zones the longitudinal axes of which are more or less parallel to the general coast line, that is, running north-west by south-east. Consequently a traveller moving eastward would pass through a series of "climates" increasing in severity just as if he were travelling northward in a region in which the zones were running eastward and westward. This unusual condition is graphically shown when the isothermal regions of Canada are plotted as in Figure 6. In this figure it is seen that the lines denoting regions of similar mean temperatures reduced to sea level values are deflected southward in British Columbia so that some of them, particularly those of 45° and 47.5°F., run almost at right angles to the general direction of the

others. Thus, portions of British Columbia are shown to have temperature conditions which normally prevail in regions much farther south. That is, the southern portion of Vancouver island and the lower mainland within the 47.5° isotherm are comparable to portions of the States of Washington and Oregon on the Pacific coast and portions of New York State on the Atlantic. In Europe the same isotherm (47.5°F.) passes through England, France and Germany.

CONDITIONS IN AQUATIC HABITATS

Effect of Air Temperature

With regard to air temperature the average maxima and minima for the district throughout the year are probably the most important factors since these are responsible for the maximum temperatures attained by the lakes in the district during the summer and for the length of time the lakes are covered with ice in the winter. Maximum summer temperatures have been recorded for only a few lakes as will be shown in the limnological data to follow. Even less is known of the winter temperature conditions since few observations have been made. However, since the duration of ice-cover provided visual evidence of the effect of winter temperatures, data regarding this condition are given in Table 1 which includes lakes at various altitudes in the four climatic belts under consideration. It will be seen that the frequency and duration of ice-cover is greatest for those lakes in the coldest climatic belts and for those at the highest altitudes within the belts. Thus, lakes near the coast are rarely completely covered with ice while those in the interior at high elevations may be ice-bound for almost half the year (20 to 25 weeks). The frequency and extent of ice-cover may be influenced by factors other than air temperature, such as area and depth of lake and exposure to prevailing winds. This is evident in the case of Okanagan and Seton lakes which would freeze over were it not for the great size and depth of Okanagan and strong wind action over Seton lake.

Effect of Precipitation

The amounts and seasonal distribution of precipitation are also important factors in so far as they affect temperature conditions of the lake through controlling the run-off. The significance of the quantity of precipitation in the form of snow is apparent since, in this form, its effect upon the lake is delayed until the melting period which may be prolonged throughout the summer. The inflow of water contributed by this source has a particularly marked cooling effect since its temperature is often much below that of ground-water from other sources. For comparative purposes, discharge data for lakes of different climatic belts are given in Table 2. Reference to this table and to the meteorological data presented in Figure 5 will show the correlation between amounts of precipitation and amounts of discharge in the three different climatic belts. The effect of delayed run-off due to larger quantities of pre-

TABLE 1. FREQUENCY AND DURATION OF ICF-COVER FOR SOME LAKES OF BRITISH COLUMBIA.

Lake	*Altitude*	*Frequency*	*Duration*
Coastal Belt			
Alta	2097 feet	Annually	14 weeks
Sooke	575 "	Occasionally	— —
Cowichan	530 "	Seldom	— —
Shawnigan	380 "	Occasionally	1 week
Lillooet	310 "	Never	— —
Deer (Burnaby)	55 "	Occasionally	1 week
Dry Belt — North			
Ootsa	2669 "	Annually	16 weeks
Francois	2375 "	"	18 "
Babine	2330 "	"	20 "
Takla	2270 "	"	18 "
Burns	2200 "	"	22 "
Stuart	2200 "	"	18 "
Fraser	2192 "	"	22 "
Seton	795 "	Never	— —
Dry Belt — South			
Belgo	3800 "	Annually	20 weeks
Glen	3500 "	"	20 "
Tyaughton	3200 "	"	16 weeks
McDonald	3000 "	"	16 "
Paul	2542 "	"	20 "
Okanagan	1130 "	Rarely	— —
Interior Wet belt			
Fish	3400 "	Annually	25 weeks
Summit (Nakusp)	2490 "	"	20 "
Slocan	1762 "	"	8 "
Kootenay	1735 "	Partially	10 "
Christina	1531 "	Annually	12 "
Arrow	1386 "	Partially	8 "
Rocky Mountain belt			
Summit (Crowsnest)	4435 "	Annually	23 weeks
Jeffrey	3500 "	"	22 "
Paddy Ryan	3000 "	"	22 "

TABLE 2. COMPARISON OF DISCHARGE DATA, AS RUN-OFF DEPTH IN INCHES ON DRAINAGE AREA, FOR COWICHAN LAKE AND SHAWNIGAN LAKE (COASTAL BELT), OKANAGAN LAKE (DRY BELT) AND KOOTENAY RIVER (INTERIOR WET BELT) FOR THE YEAR 1915. (FROM "WATER POWERS OF BRITISH COLUMBIA" WHITE, 1919).

Month	*Cowichan lake* Drainage area, 235 sq. m.	*Shawnigan lake* Drainage area, 22 sq. m.	*Okanagan lake* Drainage area, 2,750 sq. m.	*Kootenay river* Drainage area, 18,000 sq. m.
January	9.46	5.56	0.19	0.60
February	7.62	3.46	0.15	0.45
March	9.18	2.41	0.16	0.52
April	11.11	2.33	0.18	1.32
May	4.13	0.99	0.33	2.93
June	2.38	0.46	0.36	3.01
July	1.15	0.17	0.33	3.15
August	0.63	0.06	0.29	2.38
September	0.26	0.00	0.21	1.35
October	3.02	0.02	0.18	0.88
November	12.80	3.83	0.17	0.81
December	19.54	15.30	0.16	0.65
Year	81.28	34.59	2.71	18.05

cipitation being in the form of snow in the interior belts is also evident. In the Coastal belt, as shown by the discharge figures for Cowichan lake and Shawnigan lake the greatest run-off occurs during the heaviest precipitation in November and December while in the interior belts the greatest run-off is delayed until June and July when the accumulated snow is melted.

LIMNOLOGICAL CONDITIONS IN SOME BRITISH COLUMBIA LAKES

Published data concerning the physical, chemical and biological conditions obtaining within the lakes of British Columbia are limited and it is desirable to give here a short limnological account of certain typical lakes. Those selected are Cowichan lake and Shawnigan lake in the Coastal belt (Vancouver island) and Okanagan lake in the Dry belt.

COWICHAN LAKE

Cowichan lake occupies several valleys in the central mountainous region of southern Vancouver island at an altitude of 533 feet above sea level and at a point about midway between the east and west coast. It is approximately 21 miles in length with a maximum width of about 2½ miles giving a total area of 24 square miles with a maximum depth of 150 meters. A maximum temperature of 20.8°C. was found during July, 1935, with a well-developed thermocline between 15 and 20 meters (Fig. 7). Dissolved oxygen values were normal, none being found below 60% saturation. The lake water is relatively soft, containing but 20 parts per million of $CaCO_3$ in the acid condition giving a pH value varying from 6.8 to 7.6.

SHAWNIGAN LAKE

Shawnigan lake is a small body of water situated in the southern portion of Vancouver island at an elevation of 380 feet above sea level. It has an area of 2½ square miles with a maximum depth of 32 meters. A maximum water temperature of 23.3°C. was found in August, 1936 with a thermocline between the 10 and 15 meter level. Summer thermal conditions for 1935 and 1936 are shown in Figure 8. Low oxygen saturation values (below 50%) were found in the bottom layers of water where pH readings indicated a decidedly acid condition. The amount of carbonates, in the acid form, was small (12 to 14 parts per million) indicating that Shawnigan lake contains water that is even more soft than that of Cowichan lake.

OKANAGAN LAKE

Okanagan lake is a large lake lying in a long, deep valley in the southern part of the interior plateau. The length is 67 miles with an average width of 2 miles giving an area of 127 square miles. The observed maximum depth is 232 meters. A maximum surface temperature of 21.3°C. was found in August, 1935 with a thermocline between 10 and 20 meters. Typical thermal

conditions are shown in Figure 7. A minimum value of 76% saturation of dissolved oxygen was found at 175 meters. The water is alkaline with 218 parts per million of $CaCO_3$ as acid carbonate and 28 parts per million as normal carbonate giving a minimum pH value of 7.6.

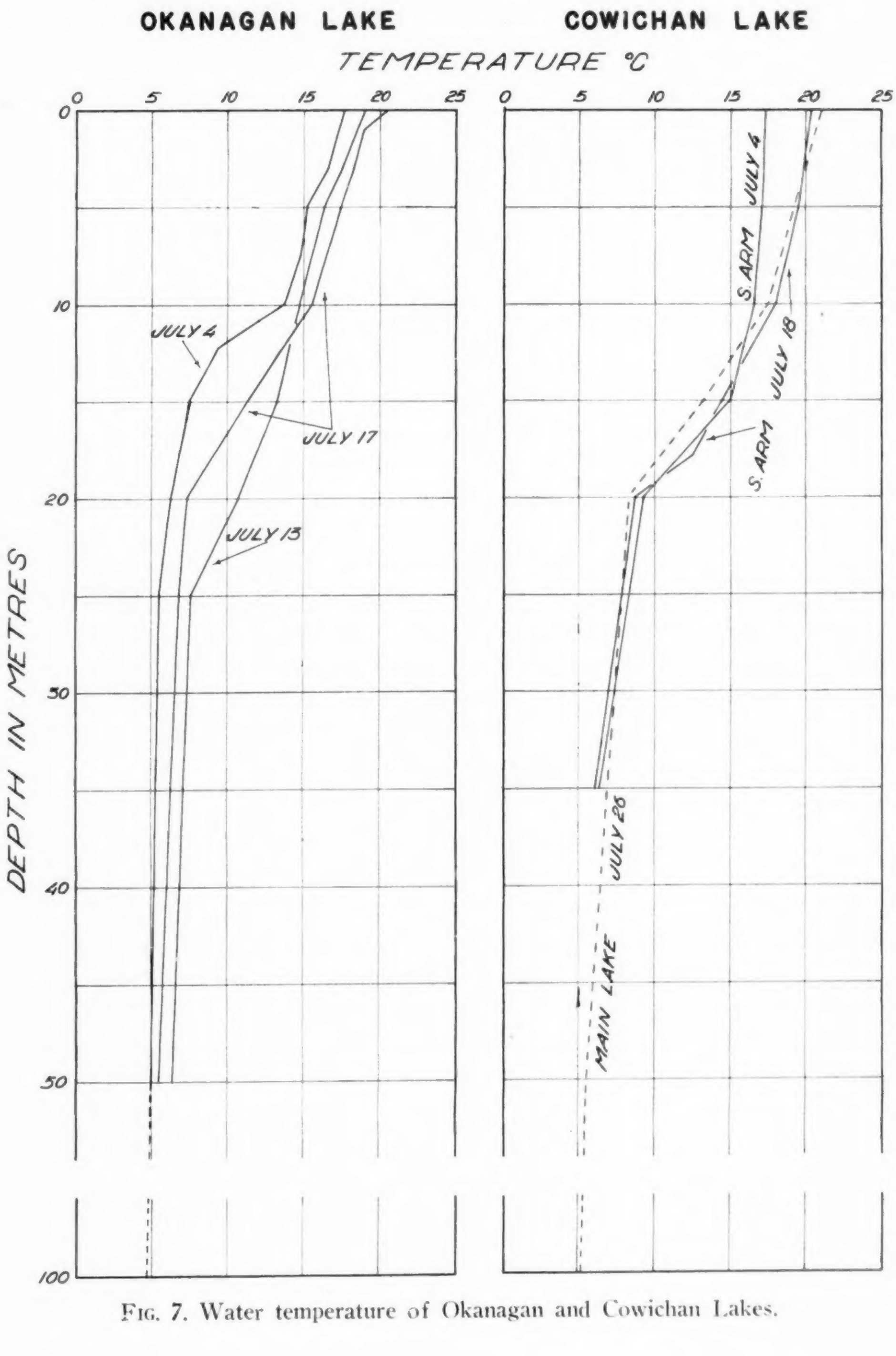

Fig. 7. Water temperature of Okanagan and Cowichan Lakes.

The limnological data pertaining to general conditions within these three lakes are presented in Table 3.

TABLE 3. COMPARATIVE DATA FOR SHAWNIGAN, COWICHAN AND OKANAGAN LAKES.

	Shawnigan	*Cowichan*	*Okanagan*
Altitude in feet	380	533	1125
Latitude	48°39′	48°30′	50°00′
Area, sq. miles	2.5	24	127
Development of shore line	3.2	3.3	3.9
Depth: maximum in metres	32	150	232
Surface temp. maximum	23.3°C.	20.8°C.	21.3°C.
Date of maximum	Aug. 4/36	July 25/35	Aug. 13/35
Bottom temp. summer minimum	6.1°C.	5.5°C.	4.5°C.
Thermocline level	5 - 15 m.	15 - 20 m.	10 - 20 m.
Frequency of ice cover	Occasionally	Seldom	Seldom
O_2 minimum in summer as %	43	60	71
pH range in summer	5.0 (?) - 7.4	6.8 - 7.6	7.6 - 8.2
Alkalinity, p.p.m. $CaCO_3$	12-14 (HCO_3)	20-22 (HCO_3)	217 (HCO_3) 28 ($CaCO_3$)
Drainage area, sq. miles	22	235	2750
Discharge (av. 3 yr. period)			
Sec. ft. per sq. m.	2.66	6.77	0.23
Depth in inches, sq. m.	34.14	91.82	2.62
Time of max. discharge	December	December	May - July

COMPARISON OF THE THREE LAKES

A comparison of these data shows that of the three lakes in nearly the same latitude, Shawnigan lake at the lowest altitude has the smallest area and least depth with a consequent higher temperature as indicated by the high maximum, 23.3°C. and high minimum 6.1°C. Moreover, the thermocline in Shawnigan lake is shallowest and the oxygen saturation is of the lowest value while the hydrogen ion concentration shows the greatest range. It has the smallest drainage area and compared with Cowichan lake in the same climatic belt it has a lesser discharge but with a maximum at the same time of year (December). Okanagan lake, since it lies in the Dry belt, differs from the other lakes in many respects. Although the surface temperature during the same season is higher than that of Cowichan lake the thermocline is less deep resulting in a lower mean temperature. This condition is indicated in Figure 7. The time of attaining maximum temperature in Okanagan lake is also at a later date (Aug. 13) and the time of maximum discharge is delayed until May, June and July. The water is more alkaline with 218 parts per million $CaCO_3$ as acid carbonate and 28 parts per million as normal carbonate, which

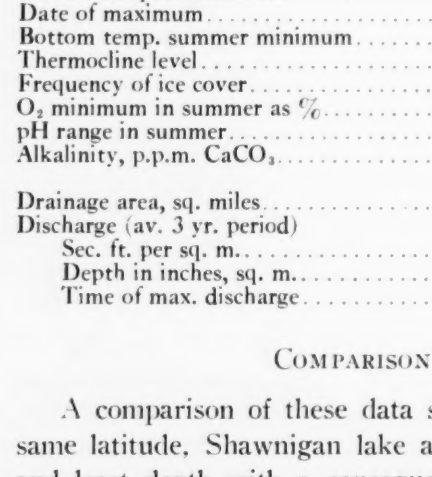

FIG. 8. Thermal conditions in Shawnigan lake, summer of 1935 and 1936.

produce a higher pH range. Of the two larger lakes neither has a complete ice-cover except on rare occasions (1893 for Okanagan) but the shore-ice persists much longer in Okanagan lake than in Cowichan lake.

CONCLUSIONS

Thus the conditions in aquatic habitats of these two climatic belts show differences which may prove to be as effective in controlling animal distribution as conditions found in terrestrial habitats of the same two belts.

GEOGRAPHICAL DISTRIBUTION

DISTRIBUTION OF CLADOCERA

Following is a list of the species of Cladocera found in British Columbia together with short notes concerning their number and distribution within the Province.

Sida crystallina (O. F. Müller). Common in all regions investigated.

Latona setifera (O. F. Müller). Collected only a few times and from widely separated lakes. It appears to be a littoral species and therefore only occasionally taken in open water.

Diaphanosoma brachyurum (Liéven). Also found in lakes of all regions.

Diaphanosoma leuchtenbergianum Fischer. Found occasionally and for short times in a few lakes of each region which supports the contention that it is a variety of the foregoing species. (Birge 1918).

Holopedium gibberum Zaddach. Widely distributed, occurring not only in the most northern lakes examined (Babine and Takla) but also in the most southern lakes (Florence and Christine). It is usually considered to be confined to the Arctic regions (Wesenberg-Lund 1908) but this does not appear to be the case in British Columbia.

Daphnia magna Straus. Collected from two localities, from ponds near Kamloops and from Becher lake, Chilcotin district. These and records in the United States do not confirm Woltereck's contention (1932) that this European species does not occur in North America.

Daphnia pulex (de Geer). Very common in certain areas, particularly in the interior of the Province. It has been found in only a few localities on the coast such as Harrison and Cultus lakes (Foerster 1925), Cowichan lake (Vancouver island) and Bullocks lake (Salt Spring island). Several undescribed varieties occur, one common form having a peculiar crown-like helmet and others approaching *clathratra* and *minnehaha* varieties (Birge 1918).

Daphnia longispina (O. F. Müller). The most common cladoceran, being found in almost every permanent body of water. In most cases the variety is *hyalina* of which the form *typica* occurs most often, particularly in the lakes of the coast and southern part of the Province. The forms *mendotae* and *galeata* are found in the more northern lakes.

Daphnia retrocurva Forbes. Recorded from the Harrison lake district (Foerster 1925).

Daphnia arcuata Forbes. Diver lake, Nanaimo (from trout stomach).

Simocephalus serrulatus (Koch). Widely distributed, as far north as the northern boundary of the Province (Dease river). It was not found in any samples from large lakes.

Simocephalus vetulus (O. F. Müller). Also widely spread out but not found as far northward as the preceding species.

Simocephalus exspinosus (Koch). One record only, from Mission slough, Okanagan lake.

Scapholeberis mucronata (O. F. Müller). Very common and widely spread, ranking next to *Daphnia longispina* in number of times collected.

Ceriodaphnia reticulata (Jurine). Commonly found in lakes of all areas.

Ceriodaphnia lacustris Birge. Common in the lakes of the Coastal and Dry belt but not found in the lakes of the Kootenay district.

Ceriodaphnia pulchella Sars. Found in the Northern Dry belt and in a few places on the coast.

Ceriodaphnia acanthina Ross. A rare species, first described from specimens collected in the Canadian prairie; found in several lakes of the Northern Dry belt and in Elbow lake (Vancouver island).

Ceriodaphnia quadrangula (O. F. Müller). Found in the lakes of the Okanagan valley and also at Kamloops and McLure (North Thompson river).

Ceriodaphnia megalops Sars. Found on one occasion in a slough near Salmon Arm (Shuswap lake).

Moina sp. probably *macrocopa* Straus. Collected from Stephenson lake (Cariboo district) where it occurred in large numbers during August, 1936.

Bosmina longirostris (O. F. Müller). Found in lakes of the Southern Dry belt and of the Coastal belt.

Bosmina longispina Leydig. Common in lakes of all districts.

Bosmina obtusirostris Sars. Less common but widely distributed in all districts.

Streblocerus serricaudatus (Fischer). Found in two collections from Vancouver island and in one from the northern interior (Francois lake).

Drepanothrix dentata (Eurén). A rare species reported only from Hicks lake (Foerster 1925) and Kawkawa lake, Hope.

Acantholeberis curvirostris (O. F. Müller). Found in one collection from Third lake (Highland district, Vancouver island).

Ilyocryptus sordidus (Liéven). One record from Devils lake near Hope.

Ilyocryptus acutifrons Sars. Recorded from Harrison lake (Foerster 1925).

Lathonura rectirostris (O. F. Müller). In one collection only, from Summit lake (Blue river district).

Eurycercus lamellatus (O. F. Müller). A large bottom-loving species, widely distributed; collected in all districts including Dease river.

Camptocercus rectirostris Schoedler. Found in collections from the Dry belt and from two localities on the coast (Kawkawa lake, Hope and Quamichan lake, Vancouver island). Two of the collections from the Dry belt (Okanagan and Long lake) are from stomachs of carp *(Cyprinus carpio)*.

Kurzia latissima (Kurz). One collection only, from a slough near Salmon Arm (Shuswap lake).

Acroperus harpae Baird. Widely distributed, having been collected in all districts except the Kootenay.

Acroperus angustatus Sars. Found in only two collections (Loop lake, Northern Dry belt and Meyer lake, Graham island).

Leydigia quadrangularis (Leydig). One record from stomach of sucker *(Catostomus macrocheilus)* Okanagan lake (Carl 1936).

Alona affinis (Leydig). A common species found in all localities.

Alona costata Sars. A smaller form, also common in all districts.

Alona guttata Sars. A less common species, found on Vancouver island and lower mainland. Collected also from Okanagan lake (Mission slough) and Dease river district.

Alona quadrangularis (O. F. Müller). A rare species collected only from the following: pond near Victoria, Cultus lake (Foerster 1925), Jones lake near Hope, Osoyoos district and Quesnel district.

Alona rectangula Sars. Also a rare species, collected from Westbank (Okanagan), Taylor lake (Princeton) and Rosebud lake (Kootenay).

Alona intermedia Sars. Found in one collection (Ootsa lake, northern interior).

Alonella nana Baird. Rarely collected probably on account of its exceedingly small size. Widely distributed; Vancouver island, lower mainland, Princeton and Dease river.

Alonella excisa (Fischer). Rare; found at Vancouver, Kamloops and Dease river.

Graptoleberis testudinaria (Fischer). A bottom-loving form rarely observed. Collected from Vancouver island (Cowichan and Sooke lake), lower mainland (Devils lake), Princeton (Lairds lake) and Cariboo district (130 Mile lake).

Dunhevedia setigera (Birge). Collected once only, McLure (North Thompson river).

Pleuroxus denticulatus Birge. A common species found on Vancouver island, lower mainland and northern interior. Not collected from the southern interior nor Kootenay district.

Pleuroxus procurvatus Birge. A less common species found in southern Vancouver island and southern and northern interior.

Pleuroxus uncinatus Baird. Found in southern Vancouver island (Thetis, Prospect and Shawnigan lakes), Salt Spring island (Blackburns lake) and Nicola valley (Trapp lake).

Pleuroxus trigonellus (O. F. Müller). Collected from Kawkawa lake (Hope), Shumway lake and Trapp lake (Nicola valley).

Pleuroxus striatus Schoedler. Found in Kawkawa lake (Hope).

Pleuroxus aduncus Jurine. Recorded from Shuswap lake from sucker stomach (Carl 1936) and collected from Lac la Hache (Northern interior).

Chydorus sphaericus (O. F. Müller). One of the most common and widely distributed species; found in bodies of water of all sizes and in all areas.

Polyphemus pediculus (Linné). Also very common and widely distributed; found in lakes of all sizes.

Leptodora kindtii (Focke). Collected in all areas; usually found in large lakes but occasionally in small lakes such as Quamichan and Prospect lakes on Vancouver island.

Distribution of Copepoda

Family Cyclopidae

The geographical distribution of the copepods of the family Cyclopidae (Genus Cyclops) is similar in many respects to that of the Cladocera. Following is a list of the species represented in British Columbia together with short notes regarding distribution as far as shown by published records and by the samples collected.

Cyclops viridis Jurine. Common in all areas and found in lakes and ponds of all sizes. The two described varieties, *americanus* and *brevispinosus*, seem to occur regardless of the size of the lake. In other localities the variety *brevispinosus* is usually found in shallow lakes or ponds (Marsh 1918). The species is also recorded by Thacker (1923) and Foerster (1925).

Cyclops biscuspidatus Claus. The most common and the most widely distributed copepod. It has been collected from 73 of the 229 lakes examined, representing every district in every area studied, except Graham island. It seems to occur in ponds or lakes regardless of size. On one occasion it was collected from Soda lake near Kamloops, the water of which contains large amounts of sodium carbonate in solution. The variety *navus* Herrick occurs in some pools.

According to Kiefer (1927) who examined and described material collected from an unnamed locality on Vancouver island, the North

American species of *C. bicuspidatus* differs from the European species in several minor respects. He describes the North American species as having a slimmer body, longer segments to the swimming feet and shorter fifth feet as compared with the European form, and accordingly assigns to it one of its former names, *C. thomasi* Forbes. However, the relationship of the two forms has been discussed by Forbes (1897) who agreed with Schmeil (1892) that the slight differences do not warrant their separation as species. Hence, it is perhaps better to retain the accepted name *C. bicuspidatus* for the North American species also.

Cyclops leuckarti Claus. Found in Trout lake, Durrance lake and Somenos lake (Coastal belt), Oyama lake and Taylor lake (Southern Dry belt), Small lake (Northern Dry belt) and Mineral lake (Rocky Mountain belt). It seems to be rather rare but widely spread.

Cyclops albidus Jurine. Very common and widely distributed having been collected from all areas examined. It seems to be characteristic of the smaller lakes and ponds where it is found near weed beds.

Cyclops fuscus Jurine. Closely allied to the preceding species, of rare occurrence. It has been collected from Sooke lake, Reservoir pool and Graham island (Coastal belt), McDonald and Trapp lakes (Dry belt).

Cyclops strenuus Fischer. Appears to be restricted to the lakes of the Northern Dry belt. It has been collected from the following lakes; Babine, Morrison, Nass, Takla, Seton and Meziadin. The last named lake lies near the coast but north of 55° latitude. Marsh (1920) found it to be common in the Arctic regions. In the United States it has been collected in the Adirondacks (Marsh 1918) and from Cayuga lake and Oneida lake, N. Y. (Marsh 1920). The above records from British Columbia appear to be the first for Canada except for those from the Arctic region.

Cyclops modestus Herrick. Has been recorded from Silver lake near Hope where it was collected on four occasions (Thacker 1923).

Cyclops serrulatus Fischer. Very common and has a wide range having been collected from lakes of all regions represented by samples. Like *C. albidus* with which it is often associated, it is found in small lakes or ponds or in weed beds of large lakes.

Cyclops prasinus Fischer. Quite common. The first published record of its occurrence in British Columbia is that of Thacker (1923) for Little lake, Hope. In the writer's collections it is found in samples from all areas except the Kootenay. It appears to be widely distributed.

Cyclops phaleratus Koch. Rather uncommon occurrence. Besides the records from Texas lake near Choate (Thacker 1923) and Trout lake (Foerster 1925) it has been found in Florence, Beaver and Elk lakes (Vancouver island), Nass, Loop and Chub lakes (Northern Dry belt) and in ponds at Kamloops. It appears to have a wide range.

Cyclops bicolor Sars. A rare copepod reported from a slough near Hope (Thacker 1923) and since been found in Timberland lakes near Ladysmith (Vancouver island) and in Okanagan lake.

Cyclops fimbriatus Fischer. Also a rare species with a distribution similar to that of the preceding species. It has been found at Choate (Thacker 1923), Timberland lake, Cowichan lake (Vancouver island) and in ponds near Kamloops.

Cyclops ater Herrick. Only two collections have contained this species, one from Bear lake, Cowichan, and the other from a pond near Lac du Bois, Kamloops. This evidence confirms Marsh's contention (1918, p. 775) that this copepod is of rare occurrence but of wide distribution.

Family Harpacticidae

Little is known of the occurrence and distribution of Copepoda of the family Harpacticidae in British Columbia possibly on account of their small size and comparative rarity in ordinary collections. Two of the following species were tentatively identified by the late Dr. Marsh and recorded by Thacker (1923); the third species was identified by Dr. R. E. Coker of the University of North Carolina.

Canthocamptus staphylinoides Pearse. Has been recorded from Devils lake, Haig (Thacker 1923), from Trout lake and Harrison lake (Foerster 1925) and from Vancouver island by Chappuis as noted by Coker (1934). It has been found by the writer in collections from Lost Lagoon (Vancouver), Madeleine lake (Vernon), and Beaver lake and Shawnigan lake (Vancouver island).

Bryocamptus hiemalis (Pearse). Found in Upper Fraser lake, Yale (Thacker 1923), in Shuswap lake, Francois lake, ponds (near Kamloops) and Long lake, Wellington.

Bryocamptus minutus (Claus). Found in large numbers in the stomachs of suckers from Shuswap lake (Carl 1936).

Family Centropagidae

The copepods of the family Centropagidae, particularly of the genus Diaptomus, occupy areas which are more restricted and well-defined than those of other families or groups of plankton Crustacea. Up to the present there have been no published records of the occurrence of any of these copepods in British Columbia except those of Thacker (1923) and Foerster (1925). The following annotated list includes the species which have already been recorded along with those records obtained from the present plankton collections. Occasional comments regarding distribution elsewhere are also included.

Epischura nevadensis Lilljeborg. Very common and appears to be widely spread. Published records include Kawkawa lake (Thacker 1923), lakes of the Harrison district and Cultus lake (Foerster 1925). It is

also found in lakes of each district in which collections have been made, except Dease river district. The northernmost record is from Takla lake (latitude 55°30′).

Heterocope septentrionalis Juday and Muttkowski. Recorded in North America on only two occasions (Juday and Muttkowski 1915, Marsh 1920). Previous to the earlier publication which first described the species, the genus was unknown in North America, being found in the northern parts of Asia and Europe only (Rylov 1930) and extending southward into Germany (Van Douwe and Neresheimer 1909). Since the first two localities in which this species was found, St. Paul island and Herschel island, are both in the far north, its discovery in Babine lake providing a third record for North America and the first for the continent proper is of considerable interest. The British Columbia record is possibly near the southern extreme of its range (Figure 9). Marsh (1920) suggests that the species is probably widely distributed across the northern part of the continent in the larger lakes.

Eurytemora affinis Poppe. Usually found in salt or brackish water and sometimes in fresh water near the sea. In British Columbia it was found on many occasions and in large numbers in Lost Lagoon (Carl 1937) and in Jericho slough at Vancouver (Fig. 9). The only other record of its occurrence on the Pacific Coast of British Columbia seems to be that of Campbell (1929) who records its presence under the name of *E. hirundoides* (Nordquist) in Alberni canal, Vancouver island. It has also been collected by Esterly (1924) from San Francisco bay. In Eurasia it is very widely distributed having been recorded from Britain (Gurney 1931), Sweden (Breeman 1908), Japan (Kikuchi 1933, 1936) and from other countries.

FIG. 9. Distribution of *Heterocope septentrionalis*, *Eurytemora affinis*, and *Diaptomus eiseni*.

Diaptomus oregonensis Lilljeborg. Most common and widely distributed species in the northern part of the United States (Marsh 1918, 1929) but found in only a small area in British Columbia. It has been taken from 14 lakes all on Vancouver island and Salt Spring island. One collection is from Deer lake near Vancouver, on the mainland, from which locality Marsh (1929) also reports it. The distribution of *D. oregonensis* in British Columbia is shown in Figure 10.

Diaptomus tyrrelli Poppe. Very common and widely spread throughout the interior of the Province in mountain areas. All of the 32 lakes in which it has been found, lie east of the Cascade mountains (Coast range) except Garibaldi lake and McDonald lake which are in the Coastal belt but at a high altitude. The distribution of this copepod is shown in Figure 11.

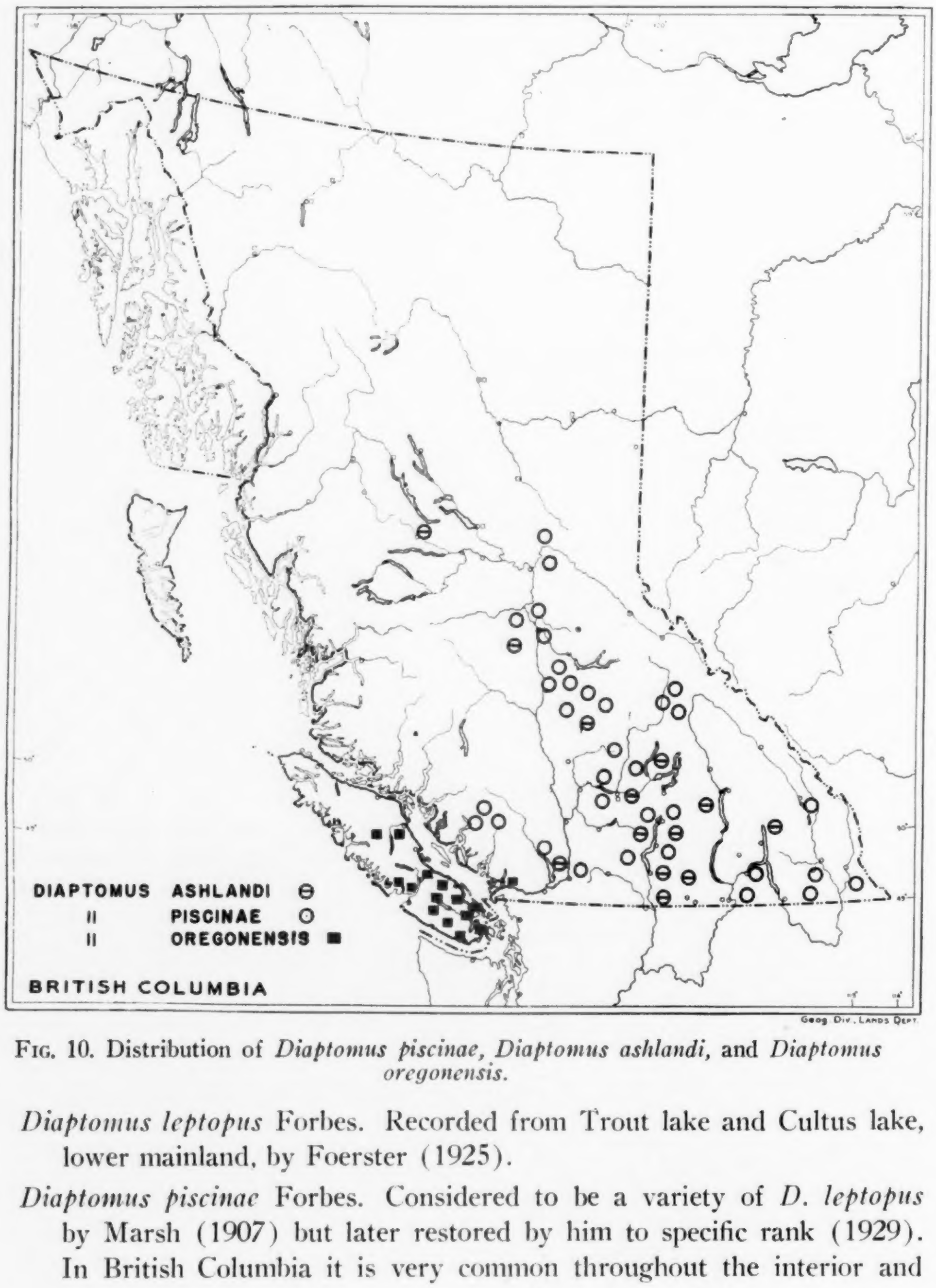

Fig. 10. Distribution of *Diaptomus piscinae, Diaptomus ashlandi,* and *Diaptomus oregonensis.*

Diaptomus leptopus Forbes. Recorded from Trout lake and Cultus lake, lower mainland, by Foerster (1925).

Diaptomus piscinae Forbes. Considered to be a variety of *D. leptopus* by Marsh (1907) but later restored by him to specific rank (1929). In British Columbia it is very common throughout the interior and

is found in a few lakes in the Coastal belt. Its distribution is illustrated in Figure 10.

Diaptomus sicilis Forbes. This small copepod which is usually a bright red in color is found in small stagnant lakes and temporary pools, on the coast and in the interior. The species is widely distributed in British Columbia as shown in Figure 12.

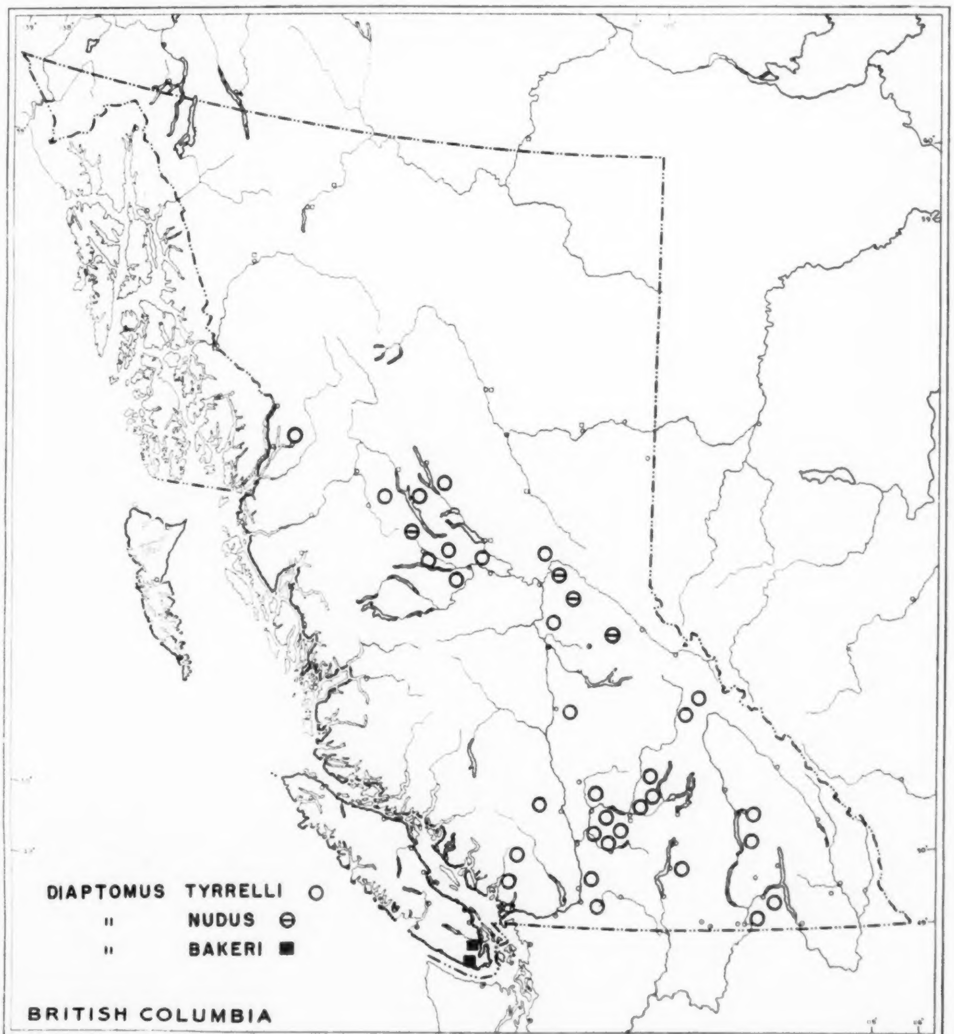

FIG. 11. Distribution of *Diaptomus tyrrelli*, *Diaptomus nudus*, and *Diaptomus bakeri*.

Diaptomus shoshone Forbes. This is one of the largest and most highly colored species of North American copepods. It has been found in only a few localities in British Columbia, viz. on Vancouver island, on the lower mainland and in the Northern Dry belt. In other parts of North America it has been recorded from St. Paul island (west of

Alaska), California, Colorado, Utah, North Dakota and once from Toronto, Ontario (Marsh 1929). Its distribution in British Columbia is shown in Figure 12.

These last two species which are closely related, are distinguished only with great difficulty and with some uncertainty, with the result that some confusion exists with regard to their distribution. A more

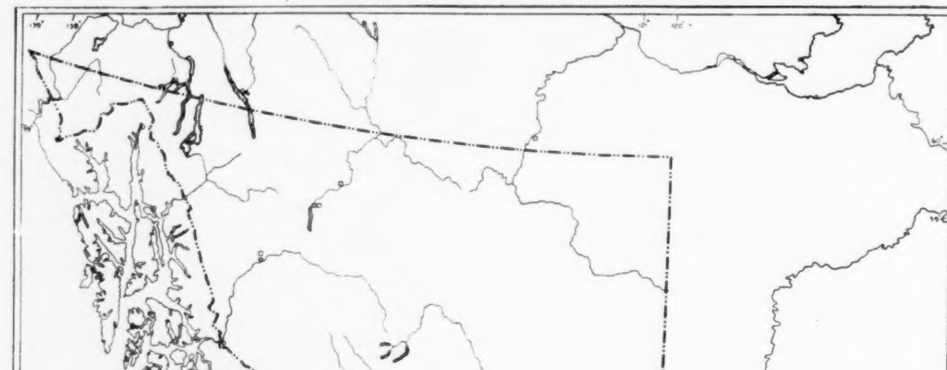

FIG. 12. Distribution of *Diaptomus denticornis, Diaptomus sicilis,* and *Diaptomus shoshone.*

intensive study of them may result in a greater degree of precision in determining their distributional range. A similar set of circumstances exists in the case of *D. leptopus* and *D. piscinae* which were considered to be varieties of a single species until recently.

Diaptomus ashlandi Marsh. This species is commonly found in the large lakes of the interior of the Province and is also recorded from Har-

rison lake and Hicks lake in the Coastal belt (Foerster 1925). It is widely distributed across the northern states westward from the Great Lakes (Marsh 1929). The distribution in British Columbia is shown in Figure 10.

Diaptomus eiseni Lilljeborg. This copepod appears to have a remarkable distribution. In British Columbia it is found in the following four lakes, all in the Dry belt: Murtle, Knouff, Paul and Swalwell. It is also recorded from Jasper Park, Alberta (Bajkov 1929). It has previously been found in North America in California (type locality), Nebraska and Labrador (Marsh 1929). A variety *occidentalis* has been described from eastern Siberia by Rylov (1922), and reported from Japan by Kikuchi (1933b). A comparison of the British Columbia specimens with a specimen from the type locality (Stanford, Calif.) and with the description of the Siberian specimens indicates that the British Columbia species varies slightly from the type species and resembles the Siberian species more closely. A similar species collected in the Canadian Arctic by Johansen and described by Marsh (1920) under the name *Diaptomus arcticus* is probably identical with this form. Unfortunately, the Arctic specimens are not available for further comparison. The present known distribution of *D. eiseni*, except for the Japanese record, is shown in Figure 9.

Diaptomus bakeri Marsh. This copepod has been found in British Columbia in only two small lakes, Prospect and Thetis, at the southern end of Vancouver island as indicated in Figure 11. According to Marsh (1929) it has been found in only two other localities, both in California near Stanford University.

Diaptomus sp. This recently described species (*pugetensis* Kincaid, in manuscript) has been found in two localities in British Columbia, in Florence lake near Victoria and in a temporary pool at Hope, as shown in Figure 13. Its distribution in the State of Washington indicates that it is probably confined to the Puget sound region.

Diaptomus nudus Marsh. This species has been found in four lakes; Burns, Aleza, Hansard and Bowron, all in the Northern Dry belt as shown in Figure 11. In the United States it has been recorded from Michigan, Colorado, Utah and Arizona (Marsh 1929).

Diaptomus signicauda Lilljeborg. This copepod has been found in only one lake in British Columbia, Meziadin lake flowing into the Nass river (Fig. 13). Other records are from California, Nevada, Colorado and Iowa.

Diaptomus siciloides Lilljeborg. This species also has been collected from only one locality in British Columbia, in an alkaline pond near Cache Creek (Fig. 13). It is widely spread throughout the United States.

Diaptomus denticornis Wierzejski. The occurrence of this copepod in British Columbia is most remarkable since it is an Old World species. Except for an unpublished record of its occurrence at Fairbanks, Alaska, by Prof. Trevor Kincaid of the University of Washington, it has not been previously recorded from North America. In British

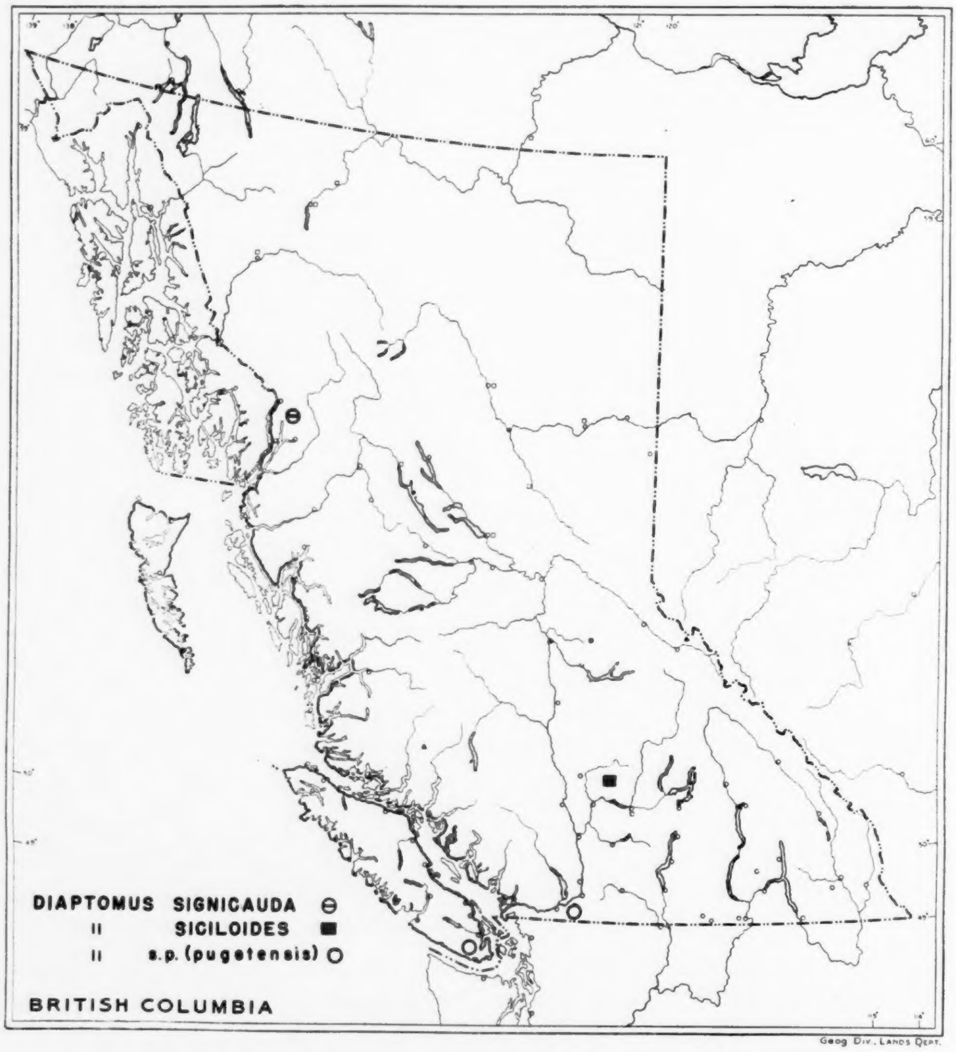

FIG. 13. Distribution of *Diaptomus signicauda*, *Diaptomus siciloides*, and *Diaptomus* sp. *(pugetensis)*.

Columbia it has been found in Burns lake, McKinley lake, Fawn lake, Small lake (near Horse lake), Anthony lake, 103 Mile lake, 105 Mile lake and Bowron lake, all in the Fraser river drainage area in the Northern Dry belt north of 51° latitude. The writer has also found this species in samples collected at Hyder, Alaska. Its distribution in British Columbia and southern Alaska is shown in Figure 11.

In Eurasia this species is recorded from Norway (Sars 1903a), Scandinavia (Ekman 1905), Alps mountains (De Guerne and Richard 1889c), Russia (Rylov 1930) and central Asia (Sars 1903b). Kikuchi (1928) reports a very closely allied species (*D. pacificus* Burckhardt) to be common in Japan. Further study may show that the British Columbia species is identical with this Japanese form and that both are referable to the common Eurasian species.

Discussion

On examining the foregoing annotated list of Cladocera and Copepoda found in British Columbia it will be noted that many of the species appear to be ubiquitous, occurring in all localities studied, while others have been taken less commonly or rarely and in widely separated areas. These rarely collected forms, in most cases, are weed-loving or bottom-loving species which may explain why they are only occasionally taken in tows through open water and also may account for their apparent scarcity and discontinuous distribution. Further collections in particular habitats and at particular seasons would probably show that these forms are as common and as widely distributed as the more well-known species. In general then, it can be said that the Cladocera and most of the Cyclopidae show little indication of being limited to particular areas; all species appear to have a wide geographic range.

Moreover, if the list of species recorded above be compared with a list of those found in Eurasia it will be seen that many species are common to both. In fact, 45 of 55 species of Cladocera and 13 of the 16 species of Copepoda (Cyclopidae and Harpacticidae) recorded from British Columbia are also found in Europe and many of them also in Asia, Africa and other parts of the world. A similar correspondence is also evident in the case of other plankton groups such as diatoms and rotifers when North American species are compared with those of other parts of the world. This remarkable cosmopolitanism of plankton organisms has long been of interest to investigators and has been aptly commented upon by Wesenberg-Lund (1908).

From the above data regarding the distribution of copepods of the genus Diaptomus three facts may be noted. First, if the distributional ranges of these copepods are compared with those of Cyclops and Cladocera in general, it will be seen that the copepods of the genus Diaptomus are not cosmopolitan in nature as are the organisms of the latter groups. That is, the species of Diaptomus occupy restricted areas that are fairly well defined and in most cases restricted to North America. Second, with a few exceptions, the various species of Diaptomus appear to occupy definite belts which seem to correspond roughly with the climatic belts previously defined. Third, certain species indicate a northern origin or center of dispersal, others suggest a southern origin while still others appear to be indigenous.

It has usually been believed that the North American and European species of Diaptomus were quite separate and that no species were common to both continents. This view was held by Tollinger (1911), Marsh (1918), Dodds (1919), Bajkov (1934) and others. However, in 1920 the European species *Diaptomus bacillifer* was found in the Canadian Arctic and at St. Paul island, Alaska and later a species collected by Dodds in the mountains of Colorado turned out to be the same (Marsh 1929). Also, in 1922 Rylov described a copepod collected in eastern Siberia as being a variety of the North American species *Diaptomus eiseni*. Thus, heretofore two species of Diaptomus had been found common to the eastern and western hemispheres. The recording of the Palaearctic species *Diaptomus denticornis* in British Columbia and Alaska provides a third copepod link between the two continents. The presence of the Eurasian genus Heterocope in British Columbia as recorded herein and the North American genus Epischura in Lake Baikal, Siberia, as recorded by Sars (1900) also suggest that other genera and species hitherto considered to be restricted to one hemisphere may in time be found to be common to both hemispheres.

Within British Columbia some species of Diaptomus appear to occupy definite climatic belts. Thus, *D. oregonensis, D. bakeri* and *D.* sp. *(pugetensis)* has been found only in the Coastal belt as shown in Figures 10, 11 and 13. Similarly, *D. tyrrelli, D. nudus, D. denticornis* and *D. piscinae* are confined to the interior with a few exceptions (Figs. 10, 11 and 12). Other species, however, such as *D. shoshone* and *D. sicilis* appear to occur both on the coast and in the interior as indicated in Figure 12. Since the two climatic belts differ mostly with regard to temperature, it is possible that this is the factor restricting the distribution of these copepods to these belts. In this regard it may be noted that according to Merriam's temperature laws (1894) as modified by Klugh and MacDougall (1924) the restriction may operate in two directions: minimum temperatures may be the controlling factors for some species while maximum temperatures may be the controlling factors for others. Thus, it appears that *D. oregonensis* may be confined to the Coastal belt on account of the too severe minimum temperatures which prevail in the interior of the Province and conversely, *D. tyrrelli* may be confined to the interior as a result of the prolonged higher temperatures of the coast. Forms such as *D. sicilis* which are found in both belts appear to be unaffected by temperature range or at least possess means of tiding over unfavorable conditions. This is substantiated by the fact that *D. sicilis* is characteristic of small ponds and temporary pools which are subject to freezing solidly in winter and drying out in summer. Thus, these copepods may be classified according to their temperature tolerances as stenothermal type including those with a narrow temperature tolerance and eurythermal type including those with a wide temperature tolerance.

This furnishes an explanation of the exceptions found in the distribution of some of the stenothermal species mentioned above. It was shown, for example, that *D. tyrrelli* was confined to the interior except for two records near the coast, viz. Garibaldi lake (alt. 4816′) and Meziadin lake (alt. 805′). The high altitude of the former and the northern latitude of the latter with consequent lower temperatures in both cases produce conditions in these lakes similar to those found in the interior.

Since the lakes of the Coastal belt and of the interior (Dry belt) differ also with regard to other factors such as alkalinity or pH it is possible that these conditions have some influence upon the distribution of these organisms. For example, it is believed by Harring and Myers (1928) that the distribution of rotifers is dependent upon hydrogen ion concentration; waters above pH 7.0 containing cosmopolitan rotifers of few species but in enormous numbers, waters below pH 7.0 containing many species but few individuals. These investigators also show that the range of pH tolerance of individual species is very narrow. In the present study it has been demonstrated that, in general, coastal lakes exhibit a lower pH range than interior lakes. This difference may play some part in determining the presence or absence of certain species but it cannot be the chief factor since all lakes in a district in which one species occurs do not have the same range in pH, indicating a fairly wide tolerance on the part of the species present in the area. Moreover, it is unlikely that pH differences which may exist between lakes of low and high altitude would explain the presence of species in lakes of high altitude and absence in lakes of low altitude.

Additional significance is seen in the distribution of these Diaptomus species in British Columbia when their ranges elsewhere are considered. As an example, it has already been shown that *D. denticornis* is widely distributed in Europe and Asia. In North America it is found in Alaska and in British Columbia as far south as latitude 51° north but apparently no further. This suggests that it has entered British Columbia from the north and has spread southward. A similar instance is seen in the case of the copepod *Heterocope septentrionalis*, former records of which are all within the Arctic zone to the north. Likewise, the copepod *Diaptomus ashlandi* is common westward across the northern tier of states from the region of the Great Lakes and through Oregon and Washington on the Pacific Coast. In British Columbia it extends up the interior at least as far north as Burns lake (54° north lat.) as shown in Figure 10. Hence, from the present known distribution the species appears to have been dispersed through British Columbia from the south. Other copepods such as *D. bakeri*, *D. piscinae*, *D. oregonensis* and *D. sicilis* also seem to have a southern origin as based on their present known distribution.

However, the distribution outside of the Province of other copepods such as *D. tyrrelli* and possibly *D. eiseni* indicates that if a center of dispersal of

these forms exists, it lies in or near the Province of British Columbia. At least, since most of the records of these copepods are from British Columbia, it suggests that these forms were possibly distributed from this area as a center, following the retreat of the ice sheet.

ALTITUDINAL DISTRIBUTION

As a result of the mountainous nature of the greater part of the Province of British Columbia, lakes and other bodies of water are found at various elevations above sea level. This is true of all areas, from the Coastal belt and through the interior, since the mountain ranges which separate the belts are several in number and are in turn separated by valleys and plateaus at various altitudes. Consequently, in any one district lakes can be found distributed from the lowest locations near the sea or in the valleys, to the highest locations atop the mountain ranges.

CLASSIFICATION OF LAKES

The lakes from which collections have been made for the present study range in elevation from sea level to 5300 feet but this range is not obtained in any one area. As example, those in the Coastal belt range from sea level to 4816 feet while those in the Dry belt are from 913 feet to 4500 feet in the south and from 795 feet to 5300 feet in the north. Moreover, since no special attempt was made to obtain samples from a graded series of lakes their vertical distribution is somewhat irregular and contains altitudinal zones represented by few or no collections. This is made evident in Table 4, which gives the number of sampled lakes in each district and their vertical distribution (White 1916).

Many attempts have been made to classify lakes according to their altitudinal range but most have been unsatisfactory since lakes do not fall into clearly recognized groups from this point of view. One of the earliest classifications was that of Ekman (1905) who grouped the lakes of northern Sweden into zones, birch (Birkenregion), willow (Grauweidenregion) and lichen (Flechtenregion) on a faunal zone basis. A similar system was used by Dodds (1919) for the Colorado lakes which he classified as plains, montane or alpine based upon an apparently natural grouping in the vertical distribution of plant life. Wesenberg-Lund (1908) has grouped lakes according to their geographic position, while other investigators have arranged them according to their size and heat content or productivity.

In the case of the lakes of British Columbia, as shown in this table, no natural classification is evident, possibly because their altitudinal range is not very extensive. However, as an aid to easy reference they may be placed in the following artificial groups:

Coastal lakes—those below 500 feet and in the Coastal belt.

Montane lakes—those between 500 and 2000 feet.

Plateau lakes—those between 2000 and 4000 feet.
Alpine lakes—those above 4000 feet.

The first group contains the largest number of lakes, all comparatively close to the sea. Most of them such as Prospect, Beaver, Thetis, Florence and Quamichan on Vancouver island and Deer, Beaver, Morris, Reservoir pond and Campus pond on the mainland are all of small size, not exceeding 900 acres in area. Others such as Shawnigan (1500 acres) and Cultus (3200 acres) are larger. Those in the second group found above 500 feet elevation may be considered to be typical mountain lakes although some of them such as the lakes of the lower Okanagan valley are in reality of the plateau type. Most of the lakes of the third group lie on elevated plains such as Forbidden Plateau on Vancouver island or Interior Plateau of the mainland. Some of these lakes, however, lie in valleys between mountains and might better be termed montane in type. Lakes of the fourth group such as Swalwell and Penask in the Southern Dry belt exhibit typical alpine conditions such as low temperature and slight stratification.

TABLE 4. NUMBER OF LAKES SAMPLED OR PROVIDING RECORDS IN EACH AREA AND THEIR VERTICAL DISTRIBUTION.

	Altitude	*Coast belt*	*S. Dry belt*	*N. Dry belt*	*Int. Wet belt*	*Rocky Mt. belt*
Alpine	5000–5500..	—	—	1	1	—
	4500–5000..	1	1	—	—	—
	4000–4500..	—	3	—	—	1
Plateau	3500–4000..	6	9	7	—	1
	3000–3500..	1	15	12	2	4
	2500–3000..	—	3	6	1	2
	2000–2500..	4	10	24	4	
Montane	1500–2000..	2	7	1	4	
	1000–1500..	5	25	1	2	
	500–1000..	16	4	2		
Coastal	S.L. – 500.	45				
	Totals.....	80	77	54	14	8

Total 233 lakes.

In addition to this altitudinal distribution these lakes also have a wide latitudinal range. Those near 54° latitude such as Babine, Takla, Francois, Burns and Hansard are over 350 miles north of those in the southern part of the Province near 49° latitude, as a consequence of which they do not lie in climatic belts which are directly comparable to those of the same elevation in the southern part.

ALTITUDINAL DISTRIBUTION OF ENTOMOSTRACA

Despite the range in elevation of the lakes studied and the consequent range in climatic conditions, plankton organisms are found in all these bodies of water. The altitudinal range of certain species of Cladocera and Copepoda

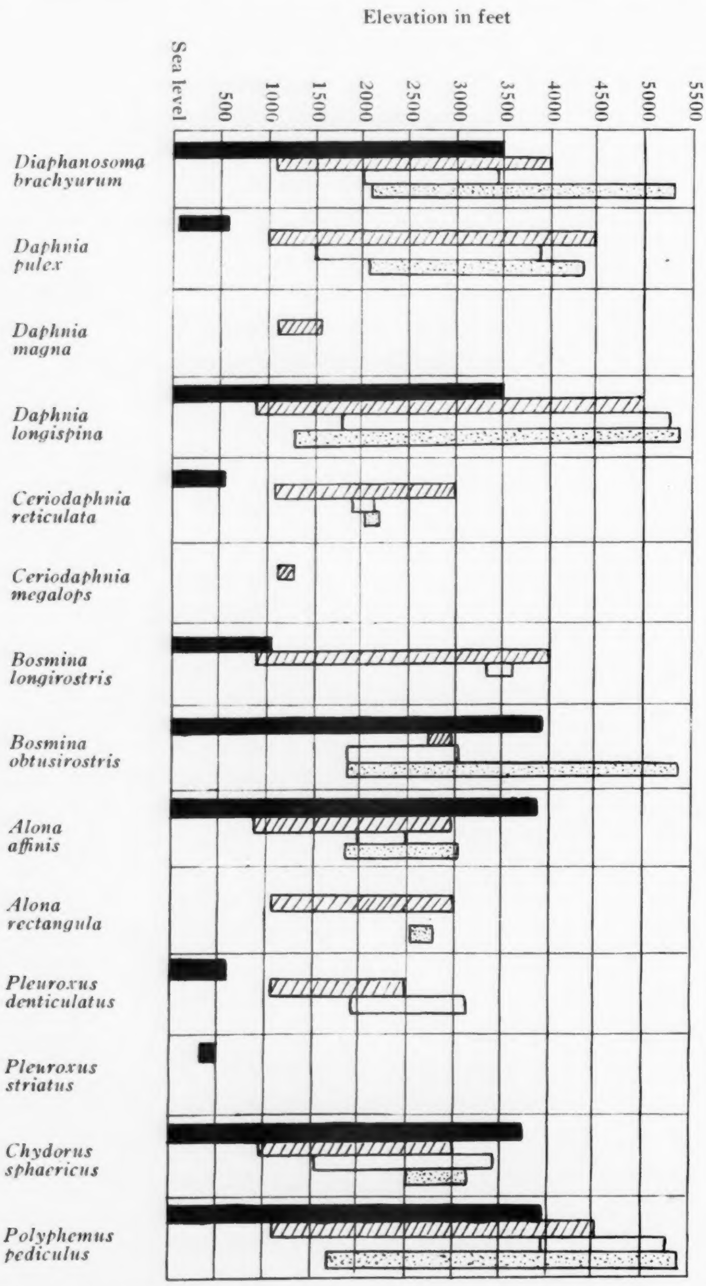

FIG. 14a. Graphic representation of altitudinal range of some Cladocera in British Columbia. Solid bars indicate range in Coastal belt; cross-hatched bars, range in Southern Dry belt; open bars, range in Northern Dry belt; dotted bars, range in Interior Wet belt and Cranbrook district.

as found in the present study is shown in graphic form in Figures 14a and 14b. Here, the vertical range in each climatic belt is shown separately, indicated in a distinguishable manner. For the sake of convenience and simplicity the Rocky Mountain belt, represented by 8 lakes in the Cranbrook district

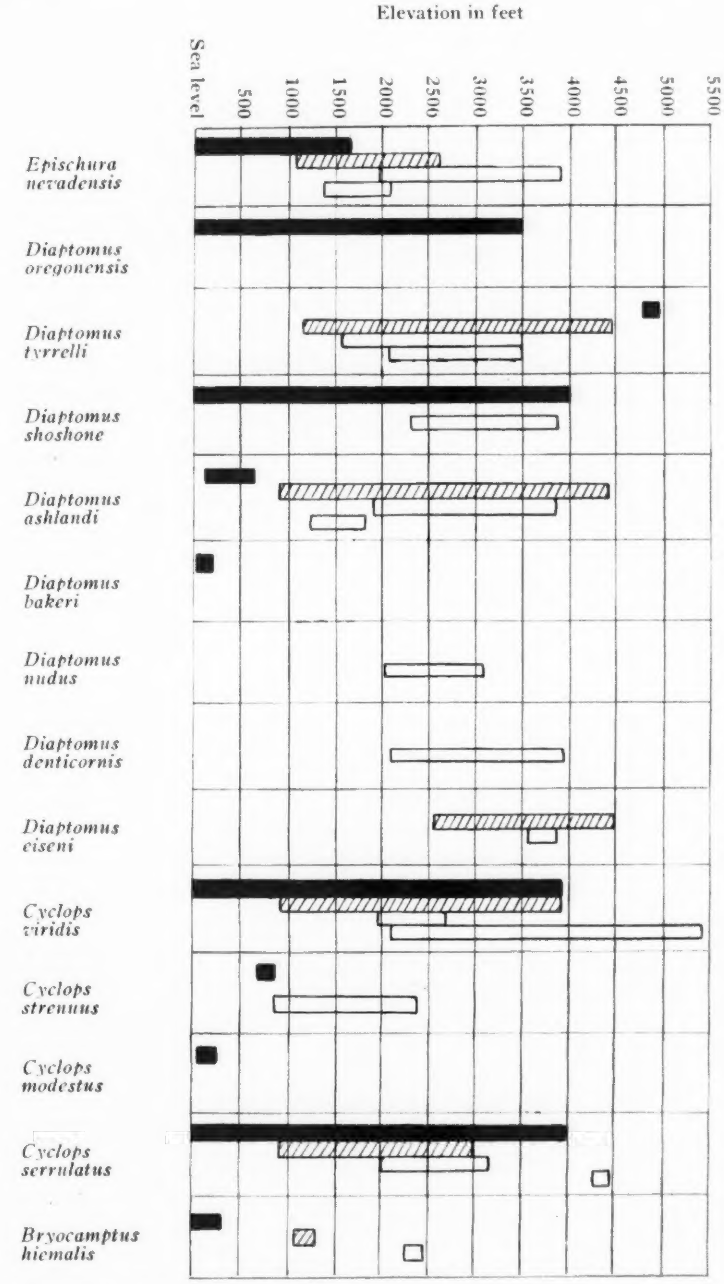

FIG. 14b. Graphic representation of altitudinal range of some Copepoda in British Columbia. Solid bars indicate range in Coastal belt; cross-hatched bars, range in Southern Dry belt; open bars, range in Northern Dry belt; dotted bars, Interior Wet belt and Cranbrook district.

is included in the Interior Wet belt. Since the number of lakes represented by collections in each zone of altitude is small, particularly at the higher elevations, there are many gaps in the ranges of most species. Consequently the record from the lowest elevation and the record from the highest elevation are taken as representing the extremes of range and it is assumed that the species is likely to be found at any intermediate point although not actually represented by samples. Therefore, the bars in Figure 14 indicate the extremes of range found for each species in each area but they do not necessarily mean that the species has been found at all the altitudes included in the bar. Conversely, the altitudes shown in the figure are not necessarily the entire range of the species; further collecting in areas of higher altitude will undoubtedly show a much more extended range than that shown by the present material. Also, as pointed out in a previous section, some of the restricted ranges are only apparent, due to the small number of collections for some species. Without doubt many of these species of apparently restricted ranges will be found to be more widely distributed than indicated in the figure. With these reservations in mind it is possible to analyze the data presented in the figure and to arrive at some conclusions regarding altitudinal distribution.

CLADOCERA

The Cladocera of British Columbia show great variety in their range of altitudinal distribution. Some species are found in lakes of the lowest altitude in each belt and extend to lakes of the highest altitude while others appear to be restricted to definite limits and in definite areas. In the former group are included *Sida crystallina, Diaphanosoma brachyurum, Holopedium gibberum, Daphnia longispina, Scapholeberis mucronata, Chydorus sphaericus* and *Polyphemus pediculus*, of which the ranges of a few are shown in Figure 14a. It will be seen that the Cladocera exhibiting the widest ranges are those that were collected in all areas and therefore are those that are most commonly found. Species with apparently narrow ranges such as *Daphnia magna, Simocephalus exspinosus* and *Ceriodaphnia megalops* are those that are rarely found. Apart from these species which seemingly occupy restricted zones it does not appear to be possible to arrange them into groups according to their limits of vertical distribution as has been demonstrated by Dodds (1919) in his study of the Entomostraca of Colorado. In this investigation Dodds showed that in the mountains near Denver, some species did not occur below an elevation of 8000 feet, others were found only above this level while still others were found at all elevations. Those species restricted to the higher levels included *Latona setifera, Holopedium gibberum, Eurycercus lamellatus, Acroperus harpae, Camptocercus rectirostris, Pleuroxus procurvatus* and *Alonella excisa* all of which are found in lakes almost at sea level in British Columbia. However, this apparent discrepancy may be explained by the fact that British Columbia lies about 500 miles north of Colorado and therefore

has a lower mean temperature at corresponding altitudes. In fact, reference to Figure 6 will show that most of the lower coastal area of British Columbia lies within the isotherm of 47.5°F. (sea level) which, according to Dodds' table (page 63), passes through the Tolland mountain region at about the 7000-foot level. Accordingly, it might be supposed that the above mentioned species have reached their lowest altitude limit and hence highest mean temperature limit at sea level in British Columbia. That this cannot be entirely true is indicated by the fact that *Holopedium gibberum* has been reported as far south as the State of Indiana (Eigenmann 1895).

Species confined to zones below 8000 feet in the Colorado mountains include *Pleuroxus denticulatus, Pleuroxus aduncus* and *Kurzia latissima* which range up to 3000 feet in the northern interior of British Columbia. In order to compare the ranges of these species in the two areas it is necessary to correct for difference in elevation and latitude. It has been calculated that for each 300-foot rise in elevation the mean temperature is lowered about 1°F. (Davis 1898). If this be accepted, then a zone at an altitude of 3000 feet in a sea-level isotherm region of 45°F. (Fig. 6) would actually have an isotherm value of 35°F. which according to Dodds' table corresponds to an altitude of about 10,000 feet in Colorado. Thus, it appears that these above mentioned species which were not found above 8000 feet in Colorado have a more extended altitudinal range and consequently a wider temperature tolerance in British Columbia.

The Cladocera of British Columbia do not show a natural grouping into well-defined altitudinal ranges as has been found in Colorado, except for a few species such as *Daphnia magna, Simocephalus exspinosus* and *Ceriodaphnia quadrangula* for which there are only a few records. This may be due to a lack of sufficiently extensive altitudinal range and hence temperature range in the localities studied, or due to an insufficient number of collections.

COPEPODA

FAMILY CYCLOPIDAE

In a similar manner the ranges of altitudinal distribution of a few copepods in British Columbia are shown graphically in Figure 14b. Examination of the data indicates that the distribution of the Cyclops species of copepods is not unlike that of the Cladocera as shown in the foregoing section. That is, the most common species such as *Cyclops viridis, C. bicuspidatus, C. albidus* and *C. serrulatus* show the widest ranges in altitudinal distribution and occur in all four climatic belts. Other species such as *C. modestus, C. bicolor, C. fimbriatus, C. ater* and *C. fuscus* which are only rarely collected appear in one or two belts only and show a comparatively narrow range in these belts. However, the disconnected nature of these restricted ranges indicates that the number of samples is not sufficiently large to give a correct indication of the true range. One exception to this generalization seems to

be evident in the case of *Cyclops strenuus*. This copepod is a northern form as shown by its geographical distribution. Its occurrence on the coast at a low altitude as indicated in Figure 14b is not inconsistent since the records are from Meziadin lake, Nass river drainage, a locality even further northward than the records from the interior.

Family Harpacticidae

The altitudinal distribution of one species of copepod *(Bryocamptus hiemalis)* representing the family Harpacticidae is also indicated in Figure 14b. Little can be said regarding the vertical distribution of this and of the other two species owing to the small number of times they have been recorded or collected. Since they have a wide geographical distribution they probably also have a wide altitudinal range.

Family Centropagidae

The copepods of the family Centropagidae, represented by four genera in British Columbia, possess peculiarities of distribution which are deserving of special consideration.

The brackish-water copepod *Eurytemora affinis* has been found only closely associated with the sea; it is unlikely that it will be found far above sea level. However, the large species *Heterocope septentrionalis* which has been recorded near sea level in the far north is found at an elevation of 2330 feet in Babine lake, its sole record to date. The closely related and very common form, *Epischura nevadensis*, is distributed in all belts with a total range from sea level to 3800 feet; no restriction to a definite zone is apparent. The vertical range of the last mentioned species is shown in Figure 14b.

With respect to the altitudinal distribution of the *Diaptomus* species of copepods a different set of circumstances is evident. The species appear to occur in definite climatic belts as pointed out in a previous section, and moreover, they appear to occur in definite altitudinal zones within these belts. Thus, one group including *Diaptomus sanguineus, D.* sp. *(pugetensis)* and *D. bakeri* occur only on the coast and at low altitudes in lakes of the coastal type. *Diaptomus oregonensis* is also restricted to the coast but it is found up to an elevation of 3500 feet in lakes of the coastal, montane and plateau types.

A second group, *Diaptomus tyrrelli, D. piscinae, D. ashlandi, D. nudus, D. denticornis* and *D. eiseni* are almost entirely restricted to the interior belts according to the data, with three exceptions, and are found at comparatively high altitudes in these belts. The exceptions include *D. tyrrelli,* found in lake Garibaldi on the coast at an elevation of 4816 feet, *D. piscinae* found in Eva and Judd lakes north of Squamish at elevations of 1550 and 1180 feet respectively, and *D. ashlandi* found in Harrison and Hicks lakes by Foerster (1925) at elevations of 30 and 540 feet respectively and 80 miles from the

coast. Since these coastal lakes are either at high altitudes and therefore of the plateau or alpine type, or removed some miles from the sea coast they lie within areas in which climatic conditions approach those of the interior which renders the occurrence of these otherwise interior copepods not inconsistent with their general range.

Of this last-mentioned group, *Diaptomus nudus* and *D. denticornis* are found only in the Northern Dry belt and within comparatively narrow limits of altitudinal range. A third group of the two species, *Diaptomus shoshone* and *D. sicilis* appear to occur at various altitudes both on the coast and in the interior. The confusion concerning the taxonomy of these last two species and also of *D. leptopus* and *D. piscinae* may account for a part of the apparently disconnected nature of their distribution.

DISCUSSION

Since the chief effect of altitude is manifest in temperature, so far as aquatic organisms are concerned, it may be supposed that temperature is the controlling factor in restricting organisms to definite altitudinal zones. Thus, the foregoing data regarding altitudinal distribution are consistent with the data regarding geographical distribution in that they confirm the hypothesis that these species of copepods fall into two types on a basis of their temperature tolerances. The stenothermal type, as shown by their restricted geographical range, is also restricted in altitudinal range, some confined to low levels, others found only at high levels. Copepods of the eurythermal type, with wide temperature tolerance, are found at all elevations.

In this respect the copepod *Diaptomus oregonensis* is an exception. It has been shown to occur not only on the coast but at elevations up to 3500 feet as on the Forbidden Plateau. Since climatic conditions are much more rigorous at this altitude it is surprising that this copepod is not also found in the interior where similar climatic conditions are found, particularly since it is common in the northern states and in the Great Lakes region of eastern Canada. Its absence from the lakes of the interior of British Columbia indicates that factors in addition to temperature influence distribution. The recognition of this fact makes it more evident that the circumstances controlling the distribution of organisms are of a complex nature.

These distributional results do not agree entirely with those of investigators in other parts. In Jasper Park, Alberta, Bajkov (1929) found *D. ashlandi* only in Maligne lake above 5500 feet elevation. This species has been found to occur almost down to sea level in British Columbia. On the other hand *D. piscinae* was found in Jasper Park only in the warmest (lowest altitude) lakes, whereas in British Columbia it is found from 1100 to 4500 feet in the coldest lakes of the plateau and alpine types. Moreover, the range of *D. tyrrelli* in British Columbia is apparently much greater than that of *D. sicilis*, which is the reverse of the case found in the Alberta investigation.

In Colorado, Dodds (1919 and 1924) found the range of *D. nudus* to be from 5000 to 11,000 feet in altitude, and classifies it as a eurythermal type. In British Columbia it appears to have a comparatively narrow altitudinal range, similar to stenothermal types. On the other hand, *D. shoshone* which appears to be of the eurythermal type in British Columbia was found to be stenothermal by Dodds.

However, these disagreements should not be considered absolute until further data concerning distribution and temperature tolerances are obtained.

INTERSPECIFIC RELATIONSHIPS

Typical Plankton Communities

A large number of species of Cladocera and Copepoda may be found in a district as a whole, but only a few of these species are found associated in various combinations in each body of water. In the examination of plankton collections from such a district one of the most striking features is that the number of species found in large lakes is relatively small when compared with the number occurring in smaller lakes. In the open waters of large lakes the species are all of the limnetic type except for occasional individuals accidentally transported from the shore zone. In the open waters of small or shallow lakes where no position is far removed from shore to bottom, many littoral species are found while in ponds almost all the species are littoral or paludinal, the proportion depending upon the size of the pond. This progressive development of the animal and plant population from a deep lake through a shallow lake to a temporary pond and finally a terrestrial habitat has been demonstrated by Eddy (1934) in his study of freshwater communities in Illinois. The relation between the number of plankton organisms and age of pond has also been shown by Shelford (1913) by the study of a series of ponds in which the numbers of animals, except fish, were found to increase with age of pond. Although the plankton population of all lakes tends to pass through these various stages of increasing numbers and variety as the lake decreases in size with age, the several stages can be seen simultaneously if a number of lakes of different sizes be examined. Table 5 shows the composition of the plankton communities found in six such British Columbia lakes varying in area from 81,000 acres to 5 acres.

From these data it can be seen that a typical plankton community of the open water of a large lake such as Okanagan or Cowichan includes *Diaphanosoma* sp., *Daphnia longispina* variety, *Bosmina* sp., *Leptodora kindtii*, either *Epischura nevadensis* or *Diaptomus* sp. (sometimes both) and one or more species of *Cyclops*. In smaller lakes such as Prospect or Aleza some of these forms are replaced or in some cases accompanied by littoral species such as *Sida crystallina*, *Ceriodaphnia* sp., *Simocephalus* sp., *Scapholeberis mucronata*, *Pleuroxus* sp. and *Chydorus sphaericus* and in the smallest bodies of water such as permanent pools almost no truly limnetic species are found.

A noticeable feature in such a comparison is the increase in variety or number of species with decrease in size of lake. A typical open-water community is composed of about 7 species while that of a pond is made up of almost twice that number. Communities in open water of lakes of intermediate size have an intermediate number of species. The relation between size and number of species is shown in Table 5. Thus, if the variety or number of species present be a measure of productivity it would seem that small lakes are much more productive per unit area than are large lakes. This is probably a direct result of the greater proportion of plant or littoral zone in small lakes as compared with large lakes which, in turn, may be the result of more favorable conditions concentrated in a smaller area.

TABLE 5. VARIETY AND NUMBER OF SPECIES IN TYPICAL OPEN WATER PLANKTON COMMUNITIES.

Organism	*Okanagan* 81,000 acres	*Cowichan* 15,000 acres	*Shawnigan* 1,500 acres	*Prospect* 300 acres	*Aleza* 100(?) acres	*Pool* 5 acres
Sida crystallina	..	..	X	X	X	X
Diaph. brachyurum	..	X	..	..	..	X
Diaph. leuchtenbergianum	X	..	..	..	..	..
Daphnia longispina	X	X	X	X	X	..
Ceriodaphnia reticulata	..	..	..	..	X	X
Ceriodaphnia acanthina	..	..	..	..	X	..
Simocephalus serrulatus	..	..	..	X	X	X
Camptocercus rectirostris	..	..	..	..	X	..
Scapholeberis mucronata	..	..	X	X	..	X
Pleuroxus denticulatus	..	..	..	X	X	..
Pleuroxus procurvatus	..	..	..	..	X	X
Pleuroxus uncinatus	..	..	..	X	..	..
Bosmina obtusirostris	..	X	X	..	..	..
Bosmina longispina	X	..	..	..	..	X
Alona affinis	..	..	..	..	X	..
Eurycercus lamellatus	..	..	..	..	X	..
Polyphemus pediculus	..	..	X	..	..	..
Leptodora kindtii	X	X	X	..	..	..
Chydorus sphaericus	..	..	..	..	X	X
Epischura nevadensis	X	..	X	X	..	X
Diaptomus oregonensis	..	X	..	..	..	..
Diaptomus bakeri	..	..	..	X	..	..
Diaptomus ashlandi	X	..	..	..	..	..
Diaptomus nudus	..	..	..	..	X	..
Cyclops bicuspidatus	X	X	X	X	..	..
Cyclops albidus	..	..	..	X	X	..
Cyclops prasinus	..	..	..	..	..	X
Cycops serrulatus	..	..	..	..	..	X
Total	7	6	8	10	13	11

With regard to lake communities it should also be noted that a genus is rarely represented by more than one species, except in the case of small lakes. Thus, although *Diaphanosoma, Ceriodaphnia, Bosmina, Diaptomus, Cyclops* and several other genera each have a number of species, more than one are seldom found in the same lake although they may be present in the same area. Examples of this peculiarity are shown in Table 5. Thus, it appears that different genera occupy different "niches" within the association and

when these "niches" are occupied by one species others are prevented from becoming established.

ASSOCIATIONS

From an examination of the distribution data it may be noted that members of certain genera and of certain species occur together in several lakes. This is particularly evident for *Heterocope septentrionalis, Epischura nevadensis* and seven species of Diaptomus all of which are found in various combinations in the lakes of the Northern Dry belt. Here 8 of the 38 lakes represented contain both *Epischura nevadensis* and *Diaptomus tyrrelli,* one other (Babine lake) contains in addition *Heterocope septentrionalis,* 4 contain both *D. piscinae* and *D. denticornis,* 2 contain both *Epischura* and *D. piscinae* and many contain other combinations. Thirty-five of the lakes contain either Epischura or Diaptomus; one contains Epischura alone; 19 contain Diaptomus alone; 14 contain both Epischura and Diaptomus and one contains all three, Epischura, Heterocope and Diaptomus. In lakes containing Epischura, only one species of Diaptomus is usually found. No lakes contain Epischura and two species of Diaptomus but one lake (Burns) contains Epischura and three species of Diaptomus. It appears that when two species of Diaptomus are together, Epischura is not found and if the dimensions of the associated species be noted it will be seen that they differ markedly in size.

TABLE 6. APPROXIMATE SIZES OF COPEPODA (TOTAL LENGTH INCLUDING RAMI).

NAME	*Male*	*Female*
Heterocope septentrionalis	4.0 mm.	4.0 mm.
Diaptomus eiseni	3.5	4.0
Diaptomus shoshone	2.7	3.0
Diaptomus piscinae	2.4	2.5
Diaptomus sicilis	1.9	2.3
Epischura nevadensis	1.8	2.1
Diaptomus denticornis	1.5	1.9
Diaptomus nudus	1.5	1.8
Diaptomus oregonensis	1.4	1.5
Diaptomus tyrrelli	1.2	1.3
Diaptomus sp. (pugetensis)	1.1	1.5
Diaptomus bakeri	1.1	1.3
Diaptomus ashlandi	0.9	0.9

From this it would seem that between planktonic species of Crustacea found in the same body of water there is some relation as to size. Thus, of the two species, *D. piscinae* and *D. denticornis* which occur most frequently together in this group of lakes, the former has a length of 2.4 mm. for the male while the latter has a length of 1.5 mm. Similarly, of the species representing the genera Heterocope, Epischura and Diaptomus found together in Babine lake, the first has a length of 4.0 mm., the second 1.8 and the third 1.2 mm. for the male. Size differences of a similar magnitude are apparent between members of all other combinations as shown by reference to Table 6 which gives approximate lengths of the species found.

The frequencies of the associations between the various members of this group of copepods are presented in Table 7. From this, it will be seen that the combination *Epischura-D. tyrrelli* occurs in 21% of the lakes, the combination *D. denticornis-D. piscinae* occurs in 11% while the combination *Epischura-D. piscinae* occurs in 6% and other combinations are less common. In each case the associated organisms differ greatly in size.

Table 7. Association Percentages between *Heterocope septentrionalis, Epischura nevadensis* and 7 Species of Diaptomus in 38 Lakes of the Northern Dry Belt.

	Epischura	D. eiseni	D. shoshone	D. piscinae	D. tyrrelli	D. denticornis	D. nudus	D. ashlandi	Heterocope
Epischura		0	0	6	21	3	3	8	3
D. eiseni	0		0	3	0	0	0	0	0
D. shoshone	0	0		3	3	0	0	0	0
D. piscinae	6	3	3		3	11	3	0	0
D. tyrrelli	21	0	3	3		0	0	0	3
D. denticornis	3	0	0	11	0		3	3	0
D. nudus	3	0	0	3	0	3		3	0
D. ashlandi	8	0	0	0	0	3	3		0
Heterocope	3	0	0	0	3	0	0	0	

In a like manner, the frequency of associations between the copepods found in 42 lakes of the Southern Dry belt is shown in Table 8. Here, the combination *Epischura-D. tyrrelli* is less frequent than found in the more northern region, being replaced by two other combinations of equal frequency, *Epischura-D. ashlandi* and *D. tyrrelli-D. piscinae*. Second in the order of frequency is the association *D. tyrrelli-D. eiseni;* others are less frequent. A noticeable fact is that *D. sicilis* was not found associated with any of the other copepods, possibly on account of its being found only in small ponds and temporary pools which do not usually contain other species. Once again the disparity in size of the associated species is made evident by reference to Table 6.

In the case of the Entomostraca of Colorado Dodds (1919) has demonstrated associations between unrelated organisms such as Daphnia and Diap-

tomus. Similar combinations are evident in the plankton communities of British Columbia lakes but since organisms of these genera are typical of all pelagic communities their occurrence together is of little significance.

Compared with the relations between the copepods in northern British Columbia a somewhat different situation appears to exist between those of the Vancouver island region. In this area the copepods *Epischura nevadensis, Diaptomus oregonensis, D. shoshone, D. bakeri, D.* sp. *(pugetensis)* and *D. sicilis* are found but the associations between them seem to be of a negative nature. Thus, of 38 lakes on the island none contain any two of these species together except three lakes, Prospect and Thetis, in each of which both *Epischura* and *Diaptomus bakeri* are found, and McKenzie lake in which *D. oregonensis* and *D. shoshone* are found. This negative association is shown in Table 9. Despite the fact that *D. oregonensis* is found in 15 of the 38 lakes and Epischura is found in 5 within the same region, the two organisms have not been found together in one lake. That this is not the result of insufficient sampling is shown by the fact that although large numbers of collections were made in both Cowichan and Shawnigan lake all from the former contained *D. oregonensis* but no Epischura while all from the latter contained Epischura but no *D. oregonensis*. Nor can the absence of either of these two species be explained by differences in physical and chemical conditions within the two lakes. Although the detailed table in a previous section shows that limnological differences do exist (Table 3), they are not so great as those in lakes within the range of these two species. It may be remembered that the geographical and altitudinal range of these two copepods has been shown to be very wide, particularly in the case of Epischura (Fig. 14b).

Table 8. Association Percentages between *Epischura nevadensis* and Five Species of Diaptomus in 42 Lakes of the Southern Dry Belt.

	Epischura	D. tyrrelli	D. piscinae	D. sicilis	D. ashlandi	D. eiseni
Epischura		2	0	0	7	2
D. tyrrelli	2		7	0	0	5
D. piscinae	0	7		0	0	2
D. sicilis	0	0	0		0	0
D. ashlandi	7	0	0	0		2
D. eiseni	2	5	2	0	2	

However, reference to the sizes of these copepods as given in Table 6 shows that whereas the associated species *Epischura-D. bakeri* and *D. shoshone, D. oregonensis* exhibit size differences comparable to those found in other combinations in other regions, the unassociated species, *Epischura* and *D. oregonensis* show much less difference in size.

A similar situation is found in the lakes of the North Dry belt already discussed. In these 38 lakes under consideration *Daphnia pulex* or *Daphnia longispina* occur in all but 4, but occur together in only one (Burns lake). Although both species are common and often vary as to size they seldom occur together except in lakes of other localities. It would seem that these two species of Cladocera and these two species of copepods interfere with one another's existence in some way such that the presence of the one in a community tends to prevent the establishment of the other.

TABLE 9. ASSOCIATION PERCENTAGES BETWEEN *Epischura nevadensis* AND FIVE SPECIES OF DIAPTOMUS IN 38 LAKES OF VANCOUVER ISLAND.

	Epischura	D. oregonensis	D. shoshone	D. sicilis	D. sp. (pugetensis)	D. bakeri
Epischura.............		0	0	0	0	6
D. oregonensis..........	0		3	0	0	0
D. shoshone...........	0	3		0	0	0
D. sicilis...............	0	0	0		0	0
D. sp. (pugetensis)......	0	0	0	0		0
D. bakeri..............	6	0	0	0	0	

DISCUSSION

In the above presentation it has been shown that the open-water plankton community consists of a number of organisms, the number increasing with decreasing size of the lake. Each species appears to occupy a definite place or niche in the ecological relationships between the various members of the community and it is suggested that this occupancy prevents the establishment of other species which would otherwise occupy the same place in the community. Evidence has been given concerning the associations and non-associations between Copepoda of the family Centropagidae and Cladocera of the

genus Daphnia and it is indicated that this phenomenon is correlated with the size of the organism.

FACTORS GOVERNING DISTRIBUTION

Among the chief factors controlling the distribution of organisms are means of dispersal and adaptability to environmental conditions. Thus, it has been argued that some animals and plants are confined to their present habitats because their further dispersal is prevented by lack of means of dispersal or presence of natural barriers or because conditions in other areas are unsuitable for their existence. Recognition of the time element as a factor determining the extent of the occupied area was given by Willis (1922). Later it was realized that these factors were in no way simple but consisted of many minor factors with varying degrees of effectiveness with the result that the present-day concept emphasizes the complexities involved. Even so, in order that a theory may be satisfactory it must explain not only the presence of an organism in a region but also its distribution within the region and at the same time explain the absence of the organism from other regions of apparently equal suitability. A few of the factors involved are noted herein, in so far as they affect the distribution of Cladocera and Copepoda in British Columbia.

MEANS OF DISPERSAL

The means of dispersal of fresh-water organisms and their remarkable power of tiding over unfavorable seasons are well known. It is evident that those Cladocera and Copepoda which have winter eggs or "resting" eggs possess marked advantages in the method of becoming distributed and the manner of this distribution has been of interest to many students. Regarding this, Tollinger (1911) emphasizes the passive methods including transport by flowing water, by birds and by winds but at the same time does not minimize the active method by way of interconnected water systems. De Guerne and Richard (1889c) stress the importance of the marine origin of the calanid Copepoda in explaining their dispersal in the past. Marsh (1907, 1918) regards water transport as a chief factor in dispersal.

Evidence of dispersal by water transport is seen in the distribution of some copepods in the interior of British Columbia. As example, *Diaptomus denticornis* is found in the North Dry belt in 9 lakes all of the Fraser river drainage (Fig. 12) but not in all the lakes of the system. Outside of the Province, however, the species occurs in other lakes not connected with this system although they may have been connected during the drainage disturbances following the ice retreat. The dispersal of other species which are now found in other drainage systems may also have been affected by this drainage disturbance. But dispersal by water transport cannot be a chief factor influencing distribution since interconnected lakes often have a plankton community differing in many respects. As example, Longbow lake which flows

into Horse lake (Northern Dry belt) possesses a plankton element composed of *Daphnia pulex*, *Ceriodaphnia* sp., *Polyphemus pediculus* and *Diaptomus piscinae* while Horse lake supports a community including *Daphnia longispina*, *Bosmina longispina*, *Epischura nevadensis* and *Diaptomus ashlandi*. Thus although organisms are undoubtedly carried continually from the former lake to the latter no organisms are common to both. Several other interconnected lakes show the same independence with regard to composition of the plankton community. It is apparent that other factors limit the distribution and occurrence of these organisms.

Moreover, by virtue of the great age of plankton organisms as a group, they have had ample time and opportunity for dispersal during the past ages, even in the Province of British Columbia, where the time interval has been more limited. One may conclude then, that the present distribution of these forms has not been so much the result of fortuitous dispersal but rather the result of the fitness of the environment or adaptability of the organisms to the environment.

An alternative explanation is offered in the following section.

POINT OF ORIGIN

Since in all probability the area concerned in this discussion was at one time rendered barren of life by the Cordilleran ice-sheet it must have been restocked from populated areas to the south and to the north, eastern areas being cut off by the Rocky Mountains. If this hypothesis be accepted it can be argued that the Cladocera and Copepoda of this area will show evidences of dispersal from these two directions. This appears to be true to some extent, for certain species such as *Diaptomus oregonensis*, *D. bakeri*, *D. ashlandi* and *D. piscinae* are common south of British Columbia, while others such as *Holopedium gibberum*, *Cyclops strenuus*, *Heterocope septentrionalis*, *Diaptomus denticornis* and *D. nudus* are found chiefly in the north. From their distribution in British Columbia it would seem that the members of these two groups have entered this area from the south and north respectively and have reached the limits of their range in some cases. Others of more universal occurrence such as the copepods *Epischura nevadensis* and *Diaptomus tyrrelli* do not indicate definite points of origin on the basis of present knowledge although the distribution of the latter species suggests that the center of dispersal may lie within the Province.

Hence, it is apparent that the distribution of these aquatic forms in British Columbia may have been influenced in the past by points of origin or centers of dispersal outside the Province.

TEMPERATURE TOLERANCE

Plankton organisms apparently differ in their ability to withstand temperature changes, some being tolerant to narrow ranges, others being tolerant to wide ranges. Thus, tolerance or intolerance to temperature changes must be a factor in determining their distribution. The general geographical

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and altitudinal ranges of the various species of Cladocera and Copepoda in British Columbia appear to be in accordance with the climatic conditions. Those found to be ubiquitous in British Columbia are cosmopolitan in distribution indicating wide temperature tolerance, while those found in restricted zones or areas are probably existing in temperature ranges within their individual tolerances. As a result of many years intensive and extensive study of the *Diaptomus* species of copepods, Marsh (1929) concluded that "without doubt the principal controlling factor in distribution is temperature. . . ." This appears to apply to general distribution in the larger areas but does not explain the discontinuous distribution within these areas which is a marked characteristic of plankton species.

Dimensions of Lakes

The size of a lake appears to play a small part in determining the species of Entomostraca occurring in the plankton community. In addition to the relation between lake size and number of species which has already been shown, there appears to be a relation between lake size and type of species. Certain organisms are found only in large lakes, others occur only in small lakes while the remainder may be found in lakes of any size. As examples of the first group the Cladocera *Eurycercus lamellatus, Leptodora kindtii* and the Copepoda *Heterocope septentrionalis, Diaptomus ashlandi, Diaptomus nudus* and *Cyclops strenuus* are found in large lakes such as Cowichan, Sooke, Okanagan, Williams and Babine lakes. Examples of those found in small lakes include *Ceriodaphnia lacustris, Diaptomus piscinae, D. shoshone, D. bakeri, D. eiseni* and *D. sicilis*. Most of the remaining species of Cladocera and Copepoda appear to occur in large or small lakes indiscriminately although weed-loving forms such as *Simocephalus serrulatus, Chydorus sphaericus* and *Cyclops albidus* are more often collected in the smaller bodies of water.

Without doubt the lake dimension having the greatest effect upon organisms is depth since this factor determines physical and chemical conditions such as stratification, low bottom temperature, stagnation, etc. Thus the dimensional factor is probably one of temperature although biotic influences may also be involved. Nevertheless, it is evident that size of lake does determine to some extent what species may be found in the plankton community with the result that certain species may occur in certain regions depending upon the magnitude of the lakes therein. This may account for the discontinuous distribution of organisms such as *Diaptomus ashlandi* (Fig. 10) found in the largest lakes and *Diaptomus sicilis* (Fig. 12) found in the smallest lakes or ponds since bodies of water suitable to these types are relatively few in number and are often widely separated.

Interspecific Relations

Since each species of animal occupies a definite place or "niche" within the community with regard to food supply or other factors, two species

normally occupying the same ecological niche will be competitors for the same food types and therefore will be mutually repellent, with the result that one species only is usually able to persist within one community. The particular species present will be partly the result of chance, being determined by the first to arrive and become established, and partly the result of their respective powers of adaptability. From this it is apparent that these interspecific relationships will determine to a large extent the species occurring within any lake. Thus, although all conditions may be favorable to the existence of an organism within a certain body of water in a region, the establishment may be impossible as a result of the presence of other species already established. This may explain the peculiar, irregular distribution of some copepods within large districts containing lakes apparently all equally favorable to their existence. The scattered occurrences of *Diaptomus nudus* (Fig. 11), *D. piscinae* (Fig. 10), *D. denticornis* (Fig. 12) and others in the Northern Dry belt are good examples of this, as is also the discontinuous distribution of *D. oregonensis* and *Epischura nevadensis* in the Vancouver island region.

CONCLUSION

The distribution of Cladocera and Copepoda in the Province of British Columbia is the result of a combination of many factors of varying effectiveness. From the evidence and arguments presented it would seem that of all the factors entailed, temperature is of prime importance in determining what species shall be present in any area and that the interrelationship with regard to food is next in importance in that it determines which of two or more species adapted to the same or similar ecological niches occur in different bodies of water within the area. Other factors are influential to a minor degree and with an effectiveness depending upon other circumstances in each case.

Although satisfactory explanations have not been deduced for all cases, the data collected and presented herein may prove useful in contributing to a clearer understanding of the problems connected with the distribution of aquatic organisms insofar as it has made apparent the complexities involved in these problems and has indicated the wide gaps in present knowledge in this field. Many unexpected complexities are thus uncovered and many courses are opened for future investigation.

SUMMARY

1. The present study deals with data on the distribution of 55 species of Cladocera and 32 species of free-living Copepoda in the lakes of certain areas in the Province of British Columbia and attempts to determine the factors influencing their distribution.

2. Much is known concerning the distribution of Entomostraca in Eurasia but somewhat less in North America and practically nothing is known in

British Columbia except for the few records occurring in the publications of Foerster, Thacker and Rawson.

3. The material for the present study was collected by means of small plankton nets sent to collectors in various parts of the Province. The samples thus collected together with published records represent 233 bodies of water from the Coast district, northern and southern Dry belt and Kootenay district. A few of the collections were from Cranbrook and Dease river district.

4. Since it has been shown by previous experience that plankton communities are relatively stable as to species present, it is concluded that samples collected by a net of small size provide reliable evidence on the distribution of the Crustacea in any area.

5. The geography of the Province is discussed with special reference to physiography and hydrography.

6. On the basis of temperature and precipitation the Province is divisible into 4 main climatic belts, Coastal belt, Dry belt, Interior Wet belt and Rocky Mountain belt.

7. Living conditions within aquatic habitats in these climatic belts are discussed with reference to the effect of temperature and precipitation on lake conditions. Special consideration is given to conditions within Cowichan, Shawnigan and Okanagan lakes. Using these as typical bodies of water it is shown that lakes of the Coastal belt have a higher mean temperature, earlier maximum temperature and less alkaline water than those of the Dry belt.

8. The geographical ranges of the Cladocera and Copepoda of the genus Cyclops are shown to be very wide and, in general, unrestricted with regard to areas or climatic belts. Most of the species of these groups are shown to be cosmopolitan in occurrence which, according to Wesenberg-Lund, is due to their great age and adaptability.

9. The geographical distribution of the Copepoda of the family Centropagidae is shown to be more restricted to well-defined areas. The ranges of most species correspond to climatic belts and the distribution of some suggests a northern origin, of others a southern origin. The remaining species appear to occur in all areas. Two of the species, *Diaptomus denticornis* and *Diaptomus eiseni* are common to Eurasia and North America; representatives of the genera Heterocope and Epischura are also found in both hemispheres.

10. From the restriction of some species of Copepoda to climatic belts it is deduced that temperature is probably the controlling factor in the distribution of these species. It appears that the species found in the Coastal belt are prevented from becoming established in the interior by the prolonged low temperatures of the interior lakes and that the species found in the interior are prevented from becoming established on the coast by the too high mean temperature of the lakes of the coast. Species occurring in both belts appear to be less affected by temperature conditions. Thus, these species may be classified according to their temperature tolerance as steno-

thermal types including those with narrow temperature tolerance and eurythermal types including those with wide temperature tolerance.

11. Since the lakes represented by collections lie at different altitudes they may be artificially classified as coastal, montane, plateau and alpine according to their elevation.

12. In general, the Cladocera and Cyclopidae are shown to have a wide altitudinal distribution in all areas which is in keeping with their wide geographical distribution. There is little indication of restriction to altitudinal zones as was found by Dodds for the Entomostraca of Colorado.

13. The altitudinal distributions of most of the centropagid copepods appear to be restricted to definite zones within climatic belts; a few (eurythermal type) are found at all elevations. The results do not entirely agree with those found for the same species in Jasper Park, Alberta, and in the mountains of Colorado.

14. Entomostraca are known to possess unusual methods of dispersal, by birds, wind and water, but by virtue of their great age these factors cannot have been of primary importance in determining their present distribution.

15. If centers of dispersal are recognized as possibilities the distributions within and without British Columbia suggest that some species of copepods, particularly of the Centropagidae, entered the Province from the south, others from the north and still others are of local origin.

16. The size of the lake, particularly depth, influences to a small extent the type of organism found. Some species are found only in large (deep) lakes; others are found in small (shallow) lakes or in lakes of all sizes. The dimension factor is probably one of temperature.

17. Typical open water plankton communities are composed of many kinds of Entomostraca but usually each genus is represented by but one species. Two related species are associated apparently only when their source of food differs and this is shown externally by a marked difference in size of the two species. The restriction of associated organisms to a definite size range limits the number of species that may occur within an area and accounts for the disconnected nature of their distribution.

18. Some species are intolerant of the presence of other closely related species, presumedly being competitors for the same source of food, and are therefore seldom or never found together within the same community. This also limits the occurrence of certain species within an area and introduces an element of chance to the final distribution of any of these mutually intolerant species.

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LIMNOLOGICAL INVESTIGATION ON TEXAS RESERVOIR LAKES

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LIMNOLOGICAL INVESTIGATION ON TEXAS RESERVOIR LAKES

INTRODUCTION

This study has been undertaken with the hope of obtaining sufficient knowledge concerning the chemical, physical, and biological factors to learn the effect these may have upon the aging of artificial reservoirs.

It is generally conceded by limnologists, biologists in general, sportsmen and laymen, that any artificial reservoir built by impounding a fresh water stream will within three to five years develop a maximum biological productivity. This maximum condition ordinarily remains during the following three to five years, at the end of which time the biological balance appears to be lost and productivity is poor. When the reservoir reaches twelve to fifteen years of age it arrives at an "aged" condition, from which it does not recover.

A series of reservoirs of different ages are included in this limnological study.

The limnology of artificial reservoirs has received little attention. Roach (1933) worked on some of the reservoirs in Ohio. A. H. Wiebe worked on Texas reservoirs while associated with the Texas State Game, Fish and Oyster Commission, during which time he made several preliminary limnological investigations. Other general pieces of comparative research in this country appear to be lacking.

The authors of this investigation are indebted to Mr. William J. Tucker, Executive Secretary of the Texas Game, Fish and Oyster Commission; to Professor Paul S. Welch, University of Michigan; to Professor Chancey Juday, University of Wisconsin; to Dr. A. H. Wiebe, Tennessee Valley Authority, Bureau of Fisheries; to Professor H. C. Bold, Vanderbilt University; and to our many associates who from time to time have rendered valuable aid.

METHODS AND EQUIPMENT

Physical

The determination of temperature at each meter of depth was made by means of a Negretti and Zambra reversing thermometer mounted in a special case. The instrument was corrected for pressure of three tons and sealed in an outer glass tube. Tropical instead of temperate thermometers must be used in Texas during the summer months.

Turbidity was determined in the field by the use of the United States Geological Survey Turbidimeter Scale. In instances when the surface waters were disturbed by winds or currents, this method could not be used success-

fully. In every case the Jackson Turbidimeter was used to check all turbidity readings at intervals of depth from surface to bottom.

The color of the water was determined by a United States Geological Survey Color Comparator. Samples with the same turbidity as the lake water were placed in the standard tube and compared with the lake sample. The lake water, filtered through extra fine quantitative filter paper, was compared with a standard filled with distilled water. In checking these two readings an accurate color determination could thus be made.

Chemical

Samples for chemical determinations were collected by means of three-liter Juday samplers attached to calibrated ropes. Determinations were made from each meter depth on each lake once a month. Routine chemical determinations made on the samples of water were: dissolved oxygen, carbon dioxide (free and bound), hydrogen-ion concentration, nitrates, nitrites, chlorides, and phosphates. Once every three months a complete mineral analysis was made of each lake. This analysis consisted of quantitative determinations of silicon, aluminum, total iron, calcium, sodium, potassium, magnesium, bicarbonates, sulphates, and manganese. Most of the chemical analyses followed the methods described in *Standard Methods for Examination of Water and Sewage* (eighth edition, 1936) or *Laboratory Manual for Chemical and Bacterial Analysis for Water and Sewage* (Theroux et al., 1936). Hydrogen-ion determinations were made by three methods: La Motte colorimeters, Hellige disc colorimeter sets, and a quinhydrone potentiometer. The amount of floating or suspended organic matter which would pass through a No. 25 silk bolting cloth net was removed with a high-speed centrifuge, dried and ignited in a Hoskins combustion furnace. Complete dissolved organic matter was not accurately determined.

Biological

Plankton determinations were made by both statistical and gravimetric methods. In the former, the organisms were removed from the water by Juday samplers and collected in No. 25 silk bolting cloth plankton nets. Thirty liters of water from each meter composed a sample, and the concentrate was preserved in formalin. Cans of water from the same levels in equal amounts were centrifuged after being run through plankton nets, the concentrate being preserved in the same manner.

Two samples from the same level in the lake were used to obtain the statistical data, one for net plankton, the other for centrifuge plankton. Due to the sparsity of certain plankters in certain lakes at various times of the year, special methods had to be employed in order to secure statistical counts. A large shallow glass cell was constructed with a capacity of one cubic centimeter. The cell was equally divided by lining into ten one-hundred cubic millimeter fields. By counting twenty fields on five separate cells of concen-

trate, using a high-power binocular microscope, accurate determinations could be made. If the total from these counts amounted to more than five thousand organisms to the liter, the standard method, employing the Whipple Micrometer and counting cell, was used. In this case three fields were counted on each of ten cells of concentrate having one cubic centimeter capacity, and the average computed in terms of organisms per cubic meter. If in the use of the shallow cell the organisms amounted to less than five thousand per liter, work with this cell was continued. This latter method of direct counts gave accurate results. Direct counting has been given preference by Juday (1922), Eddy (1934), and Raymond (1937).

Gravimetric determinations were made on net plankton and on centrifuged material collected in the same manner as those samples used for statistical counts. Each sample was dried at approximately 60° centigrade, weighed, ignited in a Hoskins furnace at about 600° centigrade, and weighed again to get loss on ignition. The large amount of silt in the water at various times of the year often hindered our obtaining results desired in the centrifuged samples. Later analyses of the ash failed to show a loss in weight because of the breaking down of inorganic materials; hence, the writers do not include any such loss in the tables.

DESCRIPTIONS OF LAKES EXAMINED

The bodies of water used in this research were Bridgeport, Eagle Mountain, and Lake Worth, all three of which serve as the municipal water supply to the City of Fort Worth, and Lake Dallas, which serves as the municipal water supply to the City of Dallas. (Fig. 1). Reservoirs in other parts of Texas as well as Caddo Lake, a natural formation, were used for comparative data.

Bridgeport, Eagle Mountain, and Lake Worth are all located in Lower Cretaceous and Pennsylvania systems. The first and largest of the series is Bridgeport, located in Wise and Jack counties, draining parts of Wise, Jack, Clay, and Montague counties. The main feed stream is the West Fork of Trinity River and its tributaries. The lake basin is on the Canyon Group in the Brad and Caddo Creek formations.

Eagle Mountain, second in the series of chain lakes, is connected to Bridgeport by the old basin of West Fork. This conduit traverses a distance of approximately forty-seven miles from its origin to Eagle Mountain, serving as a feed stream for the lake. The area of the watershed is increased by Walnut, Vale, Big Sandy, and Garret creeks, all flowing into the conduit before it enters the lake. The main body of water is in Tarrant County; the north and west channels protrude into Wise and Parker counties, respectively. The basin of Eagle Mountain is on the Trinity and Fredricksburg group in the Paluxy and Walnut formations.

Lake Worth is connected to Eagle Mountain by the old basin of West Fork at a short distance below the dam. The drainage area of the lake, in

addition to Trinity River branch, includes Cottonwood, Mill, Silver and Live Oak creeks. Lake Worth is located in Tarrant County; the major part of the basin is on the Fredricksburg group in the Walnut formation.

Lake Dallas is in the Upper Cretaceous system, the basin of the lake being in the Woodbine sands. Clear Creek and Elm Fork of Trinity River furnish the main water supply. This lake is in Denton County, the drainage area including parts of Cooke and Denton counties.

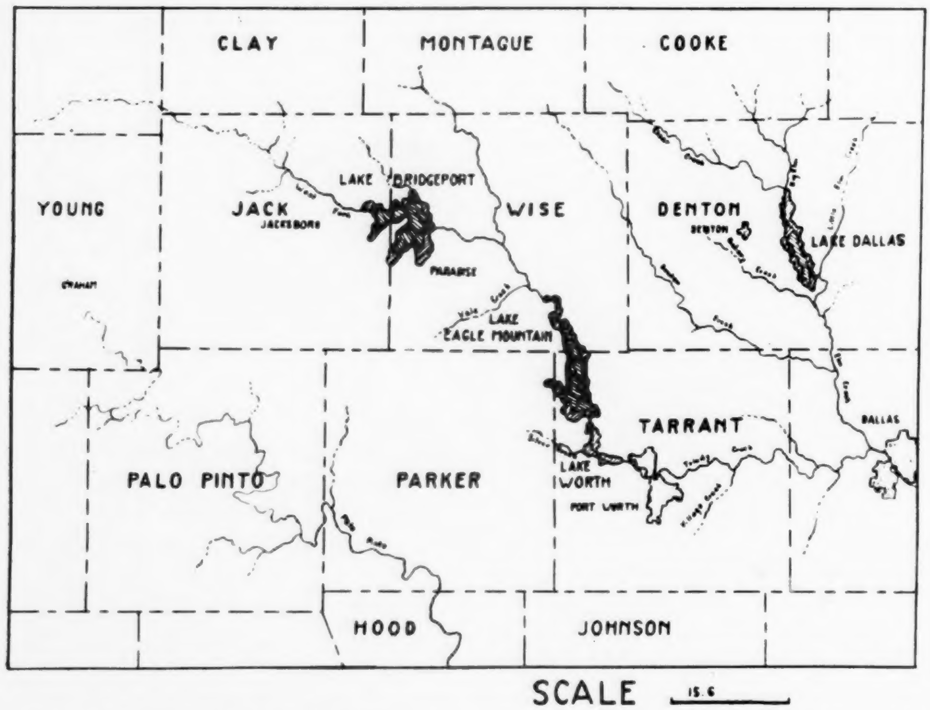

FIG. 1. Map of region showing Drainage Area (Courtesy of Major J. B. Hawley)

The composition of the various formations on which the four lakes are built and of the watershed is not the same throughout. Brad, Graford, and Caddo creeks have more limestone than do the other formations. The fact that Eagle Mountain, Bridgeport, and Lake Worth use the same water is not significant in this study. Lake Dallas, located in the Woodbine sands, presents a different condition, although the composition of the Woodbine sands does not differ noticeably from that of the Paluxy and Walnut formations which make up the basins of Eagle Mountain and Lake Worth. The watershed of Lake Dallas has less access to limestone than do the other three lakes. The watersheds of all the lakes under consideration vary greatly from year to year in respect to agriculture and general conditions, so that any present description may be partially altered during any successive year. Since, however, the area that makes up the drainage zone for the above-mentioned lakes is vast, adequate supplies of organic matter and minerals should be present for many years to come.

MORPHOMETRY

All of the morphometric data on the three lakes serving as water supply for the City of Fort Worth were obtained from Major J. B. Hawley of that city. All the figures represent engineering data obtained from the basin surveys previous to the damming of the source streams. Morphometric data on Lake Dallas were obtained by the writers from various geological publications, from the volume chart of the City of Dallas Water Supply, and by the use of Planimeters and map measurers. The rate of sedimentation of the four lakes under consideration has not been completely determined through 1938. Eakin (1936) gives data to show that in Lake Worth, the ratio of average depth of silt to average water depth is 11.7%, whereas in Lake Dallas it is 2.3%. Mr. Louis M. Glymph, of the Sections of Sedimentations Studies of the Soil Conservation Service, Washington, D. C., has made studies on the rate of sedimentation in Bridgeport, which are not available at the present time. To the knowledge of the authors, no recent complete contour maps of any of these bodies of water exist.

The comparative morphometric data are:

	Bridgeport	*Eagle Mt.*	*L. Worth*	*L. Dallas*
Maximum Length (Miles)	6	11	10	11.07
Maximum Breadth (Miles)	3	3	2	3.07
Maximum Depth (Feet)	60	50	30	40.00
Major Axis	N-S	N-S	N-S	N-S
Approximate Latitude	33°10′	32°55′	32°47′	33°20′
Approximate Longitude	97°50′	97°30′	97°27′	97°
Area (at Spillway) (Acres)	10,400	9,600	3,800	10,895
Length of Shoreline (Miles)	68	54	30	57.4
Volume (at Spillway) (Ac. Ft.)	290,000	210,000	19,000	195,000
Mean Depth (Feet)	28	22	5	17
Spillway Elevation (Feet)	668	649	594.3	525
Date Filled (Year)	1935	1934	1914	1927
Drainage Area (Sq. Miles)	1,096	794	92	1,111

PHYSICAL FEATURES

THERMAL

The time of stratification is governed by the temperature, rainfall, and wind action. Since the major axis of the lakes under consideration is north-south, it is expected that spring winds will disturb the surface water to such an extent that stratification may be delayed. Observations have been made in which stratification in progress for two weeks was suddenly disturbed by high winds. This is not usual in lakes as deep as ten meters. Since the drainage area for most of the lakes studied is large, heavy summer rains often produce unusual conditons. These are best described as various types of density currents which may, in some instances, completely upset stratification, and in other instances, induce stratification.

Thermal stratification occurs, however, during the summer season in all the lakes studied. The problem of density currents called to the attention of the authors by Professor Juday has proved interesting. Such currents in Texas reservoirs manifest themselves under two conditions. If a rain of magnitude sufficient to cause a heavy influx of water has occurred at any place on the watershed, the incoming current tends to seek a level of the same temperature in the lake. Since the feedwaters are ordinarily heavily laden with silt, thermal relations alone will not account for the distribution of the new water. If it happens that the lake is not stratified at such a time and is comparatively cool throughout, an inflow of warm water after a heavy spring rain may in a short time induce stratification. This condition will show highly turbid waters on the surface with much clearer water directly below. This stratification cannot long endure because of excess silt, and as the water loses its load of clay, the temporary stratification begins to fade. If undisturbed by winds, the silt settles slowly and equally toward the bottom, and as shown by plankton samples, may precipitate with it great masses of organic material. It does not appear, however, that this loss of organic material is permanent, since in a few weeks normal conditions return.

The second condition observed in density current activity is rather the converse of the former condition. Cold summer rains accompanied by hail often give rise to torrents of cold silt-laden waters which spread over a lake like an apron, sinking from surface to bottom and creating convection currents that completely upset both chemical and thermal stratification. Density currents also occur for no apparent reason during the fall, winter, and spring. While one portion of a reservoir may be comparatively free from excessive turbidity in the lower regions of the lake, another portion will show a large amount of fine flocculent material floating at various levels of the lake. There seems little possibility of predicting when these phenomena may occur, and in many instances it is even more difficult to determine their cause.

Temperature records in the winter often show a slight rise in the bottom water, a condition also found during a few summer months. This fact has already been noted by Wiebe in his work on the Norris Reservoir in Tennessee. Such a condition may be taken to indicate a density current or a vast collection of heavily silted water. Since all of the reservoirs under consideration are drained from the bottom, it is not unlikely that accumulations of silt and detritus cause alterations of temperature. It is interesting to observe in the late summer, when a lake is completely stratified, that this condition may be terminated by rapidly freeing two or three feet of water from the lake. It does not appear that a constant outflow will induce this condition as rapidly as does the sporadic draining of large amounts of bottom water. Most reservoirs could be prevented from stratifying by being drained at intervals of every week or so, removing large volumes of water at one time and not having a constant outflow.

Complete annual thermal conditions (shown in Figs. 2 and 3), indicate

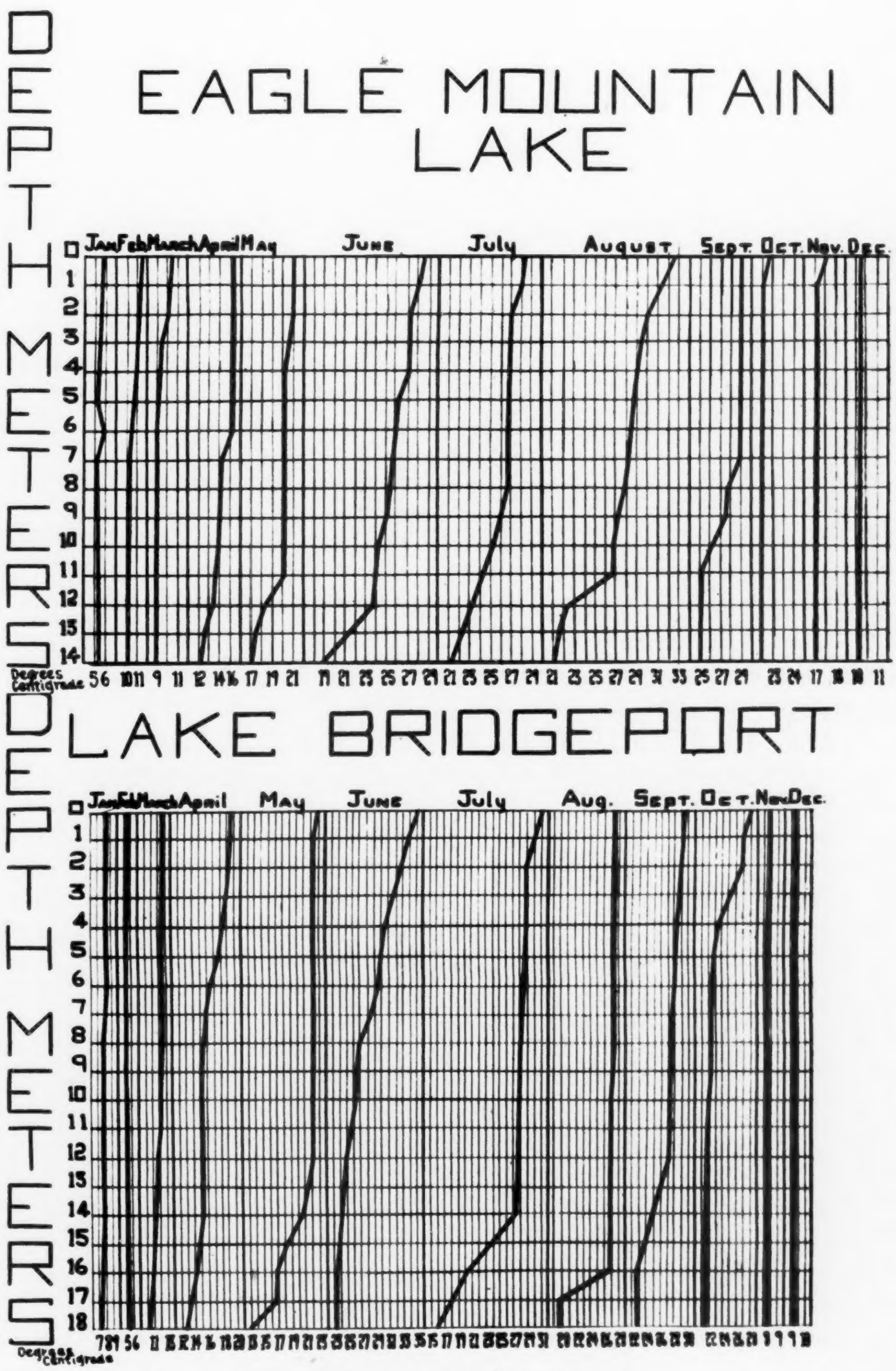

FIG. 2. Average annual temperature.

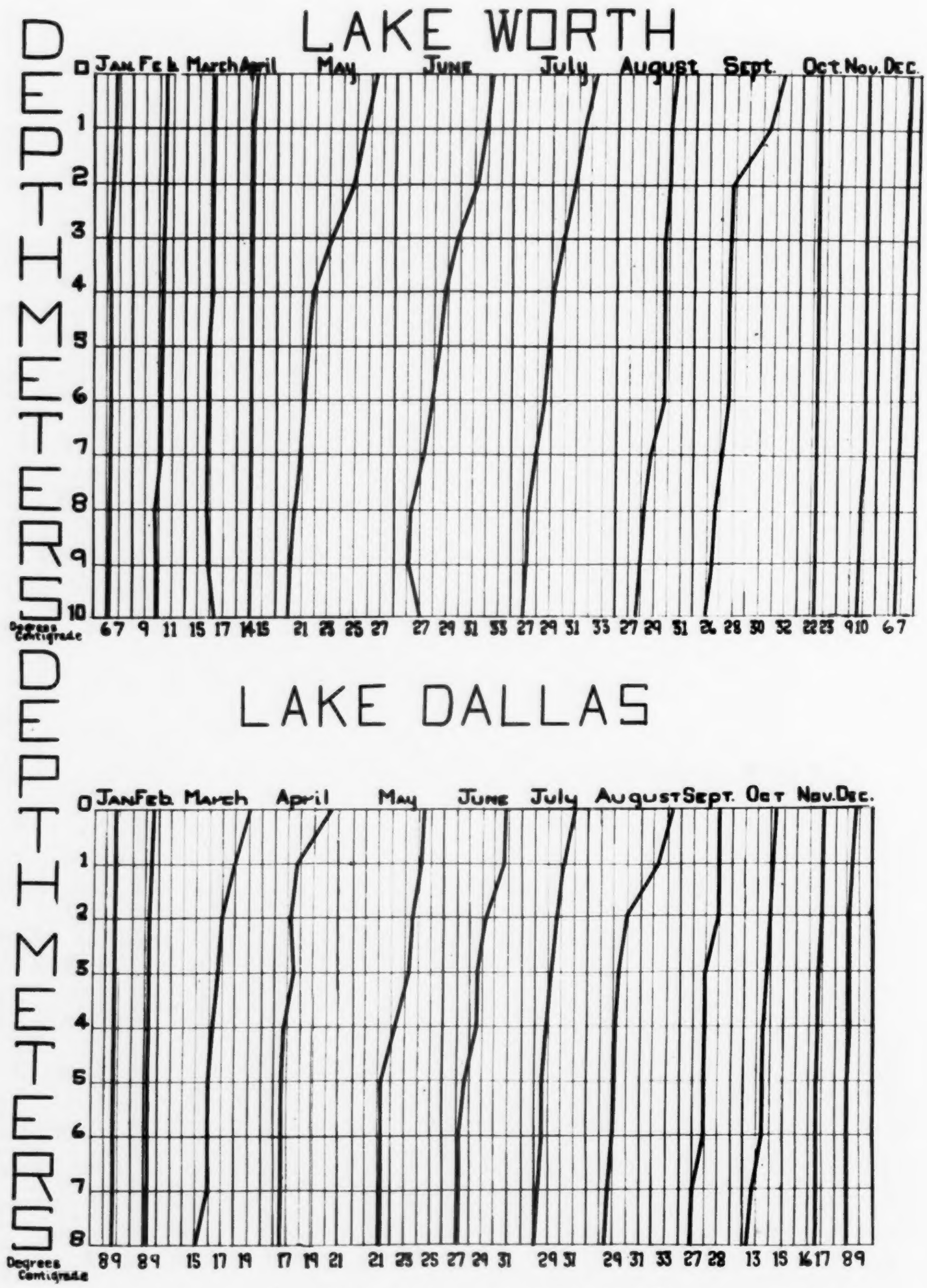

FIG. 3. Average annual temperature.

that all lakes have the same general history. The greatest temperature found was on Bridgeport during the month of June, 1937, with a surface temperature of 35°. The minimum was found on the same lake, 5.5°, in the month of February. During the course of this work ice was not found on the sur-

face waters, although weather bureau records indicate that in 1929 Lake Dallas and Lake Worth had a surface of ice two inches thick in many places.

TURBIDITY

Since many limnologists have credited turbidity as a major controlling factor in reducing productivity in water, the authors have made particular observations on this feature. Eagle Mountain, on an average, has shown less suspended material than the other lakes of the group. The silt accumulations at the bottom may become stirred so that approximately the lower meter may have a distinct rise in turbidity. The average readings for this lake, however, during a larger portion of the year, vary around 30 p.p.m., although the readings for a few summer months go as low as 15 p.p.m. Lake Worth has a turbidity slightly higher than Eagle Mountain throughout the year, because the basin is highly silted and light winds cause a rise of turbidity. However, the maximum plankton production occurs at the same time as does minimum turbidity. Lake Dallas, like Lake Worth, may become turbid in a few minutes when disturbed by a high wind, its annual turbidity being slightly higher than that of Lake Worth. The maximum plankton production was found during the time of maximum turbidity as was also found in Eagle Mountain, but not in Lake Worth. Bridgeport has more variation in the suspended material than has any of the bodies of water studied. The turbidity varied from 25 p.p.m. on the average, to 116 p.p.m. during various months over a period of two years. The greatest turbidity found in this lake was 1,100 p.p.m., which began at a depth of ten meters and extended through the sixteenth meter. The two meters below, that is the seventeenth and the eighteenth meters, had readings of only 500 p.p.m. This density current was found in March, 1938, causing a drastic reduction in oxygen, bicarbonate, and minerals in general, but raising the free carbon dioxide and hydrogen-ion content. The plankton content was reduced from a "bloom" of blue-green algae for the first ten meters to almost a complete absence of algae in the lower eight meters, a condition unprecedented in so far as this work is concerned. In general, however, the maximum amount of plankton in Bridgeport is found during the time of reduced turbidity. The annual average turbidity for the four lakes (Fig. 4) shows the general conditions described above.

The study of the turbidity in effecting productivity of lakes in Texas fails to give conclusive evidence. If the plankton content is high during excessive turbidity, it may be assumed that the plankton is contributing to the opacity of the water. If, on the other hand, the turbidity is low during high productivity, it may be assumed that such a condition is conducive to the growth of organisms. The actual conditions found show that in some lakes the turbidity is great during high productivity, and in others low during maximum productivity. Since the faunistic and floristic conditions do not differ qualitatively in the various lakes, it appears that the quantity should affect the turbidity, if organisms are assumed to account in part for the

opacity of the water. As it happens, Lake Worth with the greatest amount of plankton appearing during the month of January has a minimum turbidity. Bridgeport, on the other hand, coincident with a "bloom" of blue-green algae, had the highest turbidity ever recorded on Texas lakes. Hence conclusions must be based on further work.

The color of the water in the various reservoirs indicated in this paper varies from 15 p.p.m. to 40 p.p.m. The absence of the excessive staining of the water indicates that the watershed contains little iron and no regions of decaying vegetation. Investigations on East Texas lakes, including Caddo Lake, show highly stained water from 70 p.p.m. to 140 p.p.m. This region of eastern Texas, located in the sand, bears dense forests of pine and cypress.

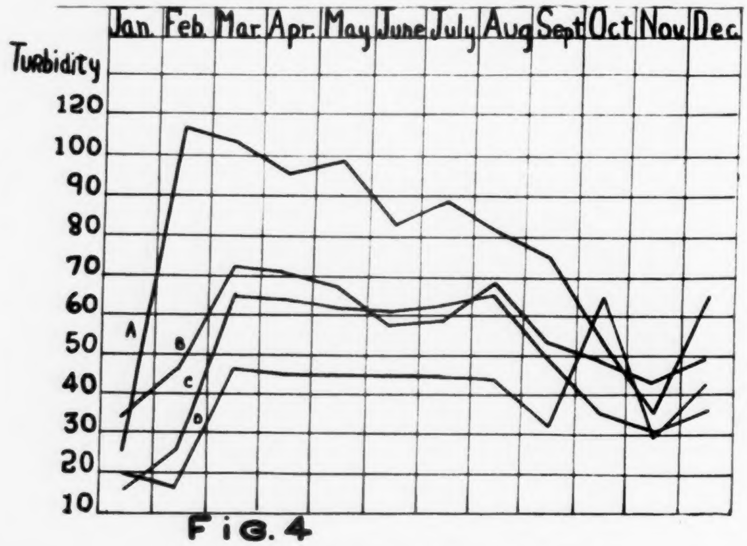

FIG. 4. Average Annual Turbidity (p.p.m.)
A. Bridgeport
B. Lake Dallas
C. Lake Worth
D. Eagle Mountain Lake

CHEMICAL FEATURES

GENERAL

Chemical work was begun by the authors early in 1936, and was continued at least once each month on the four lakes under consideration through 1938 to the present date of writing. About one thousand separate samples were analyzed for the chemical data presented in this section. Analyses of other lakes throughout the State are used for comparison. Dr. A. H. Wiebe made analyses on many of the lakes in Texas, the unpublished data of which he has given to the authors. These data will be quoted from time to time for comparison.

Dissolved Oxygen

Reduction of dissolved oxygen near the bottom of reservoir lakes begins about the middle of May and continues to July when depletion is usually accomplished. As the summer progresses, the volume of oxygen-free water increases, reaching its maximum in the latter part of August. Usually torrential rains near the first of September cause a partial return, and with the advent of cooler weather oxygen becomes equally distributed. If rains do not occur in this season, early fall winds agitate the surface sufficiently to cause a turnover. The equal distribution of oxygen may not be completely accomplished until October or November, depending upon the season. If a fall "bloom" of algae occurs in the lake, this distribution will be enhanced; or if excessive silt occurs in the flow, there may be a reduction of oxygen.

Under normal circumstances during the late fall, winter, and early spring months, lakes have an equal distribution of oxygen. As mentioned above, this condition is often disturbed by an excessive inflow of silt which settles to the bottom, increasing the rate of decomposition followed by a reduction of oxygen. Supersaturation of the lake with oxygen has been noted particularly in Bridgeport during the early spring coincident with a "bloom" of blue-green algae. This condition exists throughout the entire lake with an equal distribution of the gas. Table 1 indicates a typical condition in reservoir lakes at the four seasons of the year.

Nitrogen Compounds

Routine determinations were made for nitrites and nitrates with an occasional analysis of organic and ammonia nitrogen. In this work there does not appear to be a correlation between the various forms of nitrogen and the plankton growth. Table 1 shows a high nitrite content, often followed or preceded by a total absence of this substance irrespective of the plankton content. Nitrates appear to show variations similar to the nitrites, although not at the same time. It should be stated clearly that these analyses were not made with the intention of later correlating nitrogen and plankton. Further work on this problem may reveal a greater correlation.

Nitrite determinations were colorimetric, sulfanilic acid and alpha-naphthylamine hydrochloride being used. Nitrates were determined by using phenoldisulfonic acid, later alkalized with sodium hydroxide. Either method is sensitive, and since these samples were used fresh and often repeated, the readings of zero are taken as accurate. Evidently nitrites and nitrates in the lakes under consideration are not limiting factors.

Ammonia nitrogen varied from 0.002 to 0.9 p.p.m. in the lakes at different times during the year, usually being in greater concentration near the bottom. Organic nitrogen varied from 0.01 to 1.325 p.p.m. in the lakes generally equally distributed from surface to bottom. The greatest amounts of these were found in the midsummer and midwinter.

Free Carbon Dioxide

Free carbon dioxide was generally found in the Texas reservoir lakes. Titration, using phenolphthalein as an indicator with $\frac{N}{44}$ sodium hydroxide, the necessary milliliters being multiplied by ten, gave free CO_2 in p.p.m. According to Wiebe (unpublished), certain lakes in the western part of Texas react basic to phenolphthalein. In most instances, as shown in Table 1, the free carbon dioxide has an equal vertical distribution. During the summer, stagnation increases are often noted in the bottom layers.

Alkalinity

Since the alkalinity in the large reservoir lakes was due largely to soluble bicarbonate, it is quoted in terms of $CaCO_3$ as bicarbonates in p.p.m. The results shown in Table 1 were obtained by titrating a one-hundred-milliliter sample with .02 N H_2SO_4 using methyl orange as an indicator, the required milliliters being multiplied by ten to give the p.p.m. The reason this method was adopted rather than that suggested by Pia (1933), is that since one milliliter of .02 N H_2SO_4 is equivalent to 1 mg. $CaCO_3$, alkalinity given in terms of soluble bicarbonates is more easily applicable. If desired, the parts per million of bicarbonates as given in this paper may be changed to bound (firmly-bound) CO_2 by dividing by 2.270.

During the course of this work, the bicarbonates varied in different lakes from 54 to 194 p.p.m., or from 23.8 to 85.4 p.p.m. bound (firmly-bound) CO_2. It does not appear from the present findings that the age of the lakes affects their content. Data secured from reservoirs in East Texas show a bicarbonate content as low as 11 p.p.m., while those in central and western Texas, according to Wiebe (unpublished), agree with those in the north-central area.

Phosphates

The total phosphorus was not determined during the course of this work, but regular determinations were made of soluble phosphates. Table 1 shows that there was present an ample supply of soluble phosphates. Data from these lakes do not indicate that the rise in phosphate is coincident with reduced phytoplankton, nor its fall, with maximum phytoplankton production, as shown by Wiebe (1931). In all the lakes studied, only Bridgeport indicated a slight parallel with these findings. If more frequent determinations should be made and the nannoplankton counted accurately, possibly this condition could be shown to exist. The amount of soluble phosphorus is surprisingly high in all of these lakes, the older showing a condition not unlike the younger.

Hydrogen-ion Relations

It does not appear that the aging of larger reservoir lakes is conducive to raising the hydrogen-ion concentration. This group of lakes even during sum-

mer stagnation failed to show a pH less than 7.0 or at any time of the year more than 8.4. East Texas lakes, irrespective of age, have a pH varying from 5.8 to 7.1. Reservoirs in western and central Texas, as found by Wiebe (unpublished), agree in most respects with those worked on by the authors in north-central Texas.

MINERAL ANALYSES

Table 2 indicates the general average of mineral analyses taken from the lakes every three months. There appears to be little relation between age and the amount of calcium and magnesium in the water. Moreover, the same general statement can be made concerning the other minerals, as shown by Table 2.

In order to ascertain what proportions of the mineral content of water was shown by the analyses, the reacting or combining weights of the positive and negative elements or radicals were computed. The weights agreed so closely that the other substances present were in such small amounts that accurate quantitative tests were not attempted. Additional qualitative analyses indicated that manganese and copper were present.

TABLE 1. SURVEY OF GENERAL CHEMICAL ANALYSES.

Lake—Date	Depth Meters	Oxygen P.P.M.	NO_3 P.P.M.	NO_3 as N P.P.M.	NO_2 P.P.M.	NO_2 as N P.P.M.	Chloride P.P.M.	CO_2 Free	Bicarb. P.P.M.	Phosphate P.P.M.	pH
Bridgeport	0	6.8	0	0	.006	.002	13	3	116	.6	8.1
July 19, 1937	4	6.4	0	0	.006	.002	12	4	116	.6	8.0
	8	6.1	0	0	.006	.002	10	5	116	.6	7.9
	12	5.6	0	0	.006	.002	9.5	6	120	.6	7.8
	16	.8	0	0	.006	.002	9	9	131	.6	7.3
	18	.1	0	0	.006	.002	9	11	130	.6	7.2
Bridgeport	0	13.7	.88	.2	.0016	.0005	8	6	88	.2	7.6
Feb. 6, 1937	4	13.7	.88	.2	.0016	.0005	8	7	87	.2	7.6
	8	13.7	.88	.2	.0016	.0005	8	7	87	.2	7.6
	12	13.7	.88	.2	.0016	.001	8	7	85	.2	7.6
	16	13.6	.88	.2	.0016	.001	8	7	85	.2	7.6
	18	13.6	.88	.2	.0016	.001	8	7	85	.2	7.6
Bridgeport	0	7.8	.66	.15	.009	.003	10	4.0	96.6	.2	7.8
Oct. 2, 1936	4	7.6	.66	.15	.009	.003	10	4.0	99.2	.2	7.6
	8	6.0	.66	.15	.009	.003	10	6.0	80	.2	7.3
	12	5.1	.66	.15	.009	.003	10	8.0	60	.2	7.2
	16	5.0	.66	.15	.009	.003	10	10.0	55	.2	7.2
	18	5.0	.66	.15	.009	.003	10	12.0	54	.2	7.2
Bridgeport	0	10.6	.13	.03	.019	.006	11	4	112	.2	7.1
Nov. 30, 1937	4	10.5	.13	.03	.019	.006	11	4	112	.2	7.1
	8	10.5	.13	.03	.019	.006	11	4	112	.2	7.0
	12	10.4	.13	.03	.019	.006	11	4	112	.2	7.1
	16	10.4	.13	.03	.019	.006	11	4	112	.2	7.2
	18	10.4	.13	.03	.019	.006	11	4	111	.2	7.2
Eagle Mountain	0	10.4	Trace	Trace	Trace	Trace	21	3	134	.3	7.63
Feb. 12, 1938	4	10.6	"	"	"	"	21	3	134	.3	7.63
	8	10.5	"	"	"	"	21	3	134	.3	7.63
	12	10.5	"	"	"	"	21	3	134	.3	7.63
	14	11.0	"	"	"	"	21	2	135	.3	7.63

Table 1—*Continued.*

Lake—Date	Depth Meters	Oxygen P.P.M.	NO_3 P.P.M.	NO_3 as N P.P.M.	NO_2 P.P.M.	NO_2 as N P.P.M.	Chloride P.P.M.	CO_2 Free	Bicarb. P.P.M.	Phosphate P.P.M.	pH
Eagle Mountain	0	7.0	0	0	0	0	23	4	138	.18	7.9
July 12, 1937	4	5.7	0	0	0	0	23	5	137	.18	7.8
	8	2.6	0	0	0	0	22.5	6	140	.18	7.7
	12	0	0	0	0	0	22.0	14	151	.18	7.3
	14	0	0	0	0	0	21.5	16	161	.18	7.2
Eagle Mountain	0	6.6	0	0	0	0	23	6	137.5	.26	7.6
Oct. 2, 1937	4	6.6	0	0	0	0	23	6	137.5	.26	7.6
	8	6.3	0	0	0	0	23	6	138.5	.26	7.6
	12	6.3	0	0	0	0	23	6	138.5	.26	7.6
	14	5.8	0	0	0	0	23	6	139	.26	7.6
Eagle Mountain	0	10.2	.35	.08	.0082	.0025	21	4	143	.31	7.67
Dec. 8, 1937	4	10.2	.35	.08	.0082	.0025	21	4	143	.31	7.2
	8	10.2	.35	.08	.008	.0025	21	4	143	.31	7.2
	12	10.2	.35	.08	.008	.0025	21	4	143	.31	7.4
	14	10.2	.35	.06	.008	.0025	21	4	135	.31	7.2
Lake Worth	0	11.1	0	0	.0082	.0025	19	4	135	.16	8.0
Feb. 5, 1938	4	11.1	0	0	.0082	.0025	19	4	135	.16	8.0
	8	11.1	0	0	.0082	.0025	19	4	135	.16	8.0
	10	11.2	0	0	.0082	.0025	19	2	135	.16	7.9
Lake Worth	0	6.8	0	0	0	0	17.5	2	126.5	.38	8.0
July 27, 1937	4	5.5	0	0	0	0	17.0	6	126.8	.38	7.7
	8	.8	.013	.003	.006	.002	17.0	14	138.0	.24	7.3
	10	.6	.013	.003	.06	.02	17.4	19	144.0	.20	7.3
Lake Worth	0	7.6	0	0	0	0	16	6	132	.12	8.0
Oct. 9, 1937	4	7.4	0	0	0	0	16	6	132	.12	8.0
	8	7.2	0	0	0	0	16	7	132	.12	7.8
	10	7.2	0	0	0	0	16	7	131	.12	7.8
Lake Worth	0	11.6	0	0	0	0	18	2	129	.21	7.6
Dec. 18, 1937	4	11.5	0	0	0	0	18	2	129	.21	7.6
	8	11.5	0	0	0	0	18	3	129	.21	7.66
	10	11.4	0	0	0	0	18	3	129	.21	7.68
Lake Dallas	0	11.2	.1	.024	.018	.0055	24	4	127	.30	7.7
Jan. 5, 1938	4	11.2	.1	.024	.018	.0055	24	4	127	.30	7.7
	8	11.2	.1	.024	.018	.0055	24	4	127	.30	7.7
	10	11.2	.1	.024	.018	.0055	24	4	126	.30	7.7
Lake Dallas	0	7.0	0	0	0	0	28	4	177	.16	8.0
June, 21, 1936	4	6.0	0	0	0	0	28	6	181	.16	7.7
	8	3.0	0	0	0	0	26	8	187	.18	7.7
	10	1.2	0	0	0	0	18	14	192	.20	7.7
Lake Dallas	0	8.0	1.9	.44	.09	.026	27.6	2	131.5	.68	8.1
Aug. 13, 1937	4	7.0	1.9	.44	.04	.014	27.0	3	120	.72	7.8
	8	3.6	1.9	.44	0		26.0	7	130	.80	7.4
	10	2.2	1.9	.44	0		25.7	11	133	.92	7.4
Lake Dallas	0	9	.0088	.002	.0042	.0013	25	6	127	.20	8.0
Nov. 3, 1937	4	9	.0088	.002	.0042	.0013	25	6	127	.20	8.0
	8	8 6	.0088	.002	.0042	.0013	25	8	127	.20	7.6
	10	8.0	.0088	.002	.0042	.0013	25	8	128	.20	7.8

Table 2. Mineral Analyses.

Lakes	Silica SiO_2 P.P.M.	Aluminum P.P.M.	Total Iron P.P.M.	Calcium P.P.M.	Sodium P.P.M.	Potassium P.P.M.	Magnesium P.P.M.	Sulphate P.P.M.
Bridgeport......	5.0	10.1	.23	34.4	4.6	1.6	5.44	35.4
Eagle Mountain.	4.17	9.10	.58	36.1	3.8	1.0	8.7	14.4
Lake Worth.....	5.88	11.70	.18	47.1	4.0	1.6	4.6	21.9
Lake Dallas.....	5.6	48.03	1.05	48.1	2.6	.8	3.0	21.8

Since the mineral analyses do not indicate sufficient differences between old and young reservoir lakes, the authors cannot hold to the contention that productivity in these aquatic habitats is reduced by insufficient dissolved inorganic materials. It is highly possible that larger reservoir lakes differ from smaller reservoirs only because of the great variations in the areas of watershed. Since analyses of the streams feeding all of these lakes continue to show a mineral content often higher than that of the lake proper, it is obvious that as long as this condition exists, minerals will not prove to be limiting factors in productivity.

BIOLOGICAL FEATURES

VEGETATION*

Owing largely to the diverse ages of the four reservoirs examined, their vegetation is varied. The basins of Bridgeport, Eagle Mountain, and Lake Dallas were known to the senior author before dams were constructed across the several streams to produce lakes. Since the establishment of these lakes, various plants have appeared, and as expected, the older basins support a greater variety and a greater quantity of plants than do the younger basins.

In Bridgeport, there are approximately nine different species of submerged, floating, or emergent vegetation. The area covered by this vegetation is almost negligible, leaving vast regions of naked shore line and shoal. Since the establishment of this lake, the water level has fluctuated greatly, producing a condition unfavorable to plant growth. In certain of its parts there are remains of the terrestrial vegetation which occupied the basin before the water level was raised, and these serve as zones of protection for certain plankters and redds of spawning fish.

ANNOTATED LIST OF BRIDGEPORT VEGETATION

Nitella sp.
Equisetum hyemale L. var. *robustum* (A. Br.) A. A. Eaton (Equisetum prealtum Raf.)
Potamogeton americanus Cham & Schlecht. (Potamogeton lonchites Tuckerm.)
Dichromena sp.
Scirpus validus Vail.
Lippia lanceolata Michx. var. *recognita* Fern & Grisc.
Salix nigra Marsh
Polygonum incarnatum Ell.
Rorippa nasturtium-aquaticum (L.) Schinz & Thell. (*Nasturtium officinale* R. Br.)

Eagle Mountain, although only one year older than Bridgeport, supports sixteen different species, with a greater quantity of many of the species in different regions of the lake. Regardless, however, of the comparative increase of vegetation, the entire amount is reckoned as occupying less than 1% of the area of the basin. This lake has not been subjected to great varia-

* Source of identification: North Texas State Teachers College Herbarium; Albert Ruth Herbarium, Fort Worth Botanic Garden; Herbarium of Wm. L. McCart (private; matched specimens from National Herbarium).

tions in water level, since its source of water is largely controlled from Bridgeport. No doubt its more constant water-line has aided in the establishment of plant life. Even so, long reaches of shoal and shore line are found which are bare of vegetation. Some areas, as in Bridgeport, still have the remains of the terrestrial vegetation which occupied the basin previous to its filling.

Annotated List of Eagle Mountain Vegetation

Nitella sp.
Equisetum hyemale L. var. *robustum* (A. Br.) A. A. Eaton (Equisetum prealtum Raf.)
Potamogeton americanus Cham & Schlecht. Potamogeton lonchites Tuckerm.)
Carex emoryi Dewey
Carex Blanda Dewey
Dichromena sp.
Fimbristylis autumnalis (L.) R. & S.
Scirpus validus Vail.
Rorippa nasturtium-aquaticum (L.) Schinz & Thell. (*Nasturtium officinale* R. Br.)
Lippia lanceolata Michx. var. *recognita* Fern & Grisc.
Lemna minor L.
Heteranthera limosa (SW.) Willd.
Juncus marginatus Rostk. var. *setosus* Coville (Juncus setosus (Coville) Small.)
Salix nigra Marsh.
Polygonum incarnatum Ell.
Lippia incisa (Small) Tidestrom.

Approximately fifty-two species of aquatic vegetation are found in Lake Dallas. The general estimate is, that approximately 5% of the basin of this lake supports vegetation, a much higher proportion than that of the other two lakes. Most of the shoal region and shore line are protected from excessive wave action, yet there remain sufficient open areas of sand, mud, and gravel for zones of production, spawning beds, and for general requirements of plant growth.

Annotated List of Lake Dallas Vegetation

Marsilea sp.
Potamogeton pectinatus L.
Potamogeton americanus Cham & Schlecht. (Potamogeton lonchites Tuckerm.)
Echinodorus cordifolius (L.) Griseb
Echinodorus radicans (Nutt.) Englem.
Sagittaria arifolia Nutt.
Paspalum pubiflorum Rupr.
Zizaniopsis miliaceae (Michx.) D. & A.
Carex Brittoniana Bailey
Carex mesachorea
Carex rosea Schk.
Equisetum hyemale L. var. *robustum* (A. Br.) A. A. Eaton (Equisetum praealtum Raf.)
Alisma subcordatum Raf.
Paspalum floridanum Michx.
Paspalum stramineum Nash.
Carex Davisii Schwein & Torr.
Carex microdonata (Torr & Hook.)
Carex vulpinoidea Michx.
Cyperus acuminatus Torr & Hook.
Cyperus haspan L.
Fimbristylis autumnalis (L.) R & S.
Scirpus validus Vail.

Eleocharis sp.
Lemna minor L.
Juncus effusus L.
var. *solutus* Fern. & Wiegand
Juncus marginatus Rostk.
Salix nigra Marsh
Polygonum lapathifolium L.
Polygonum ramosissimum Michx.
Rorippa nasturtium-aquaticum (L.) Schinz & Thell. (*Nasturtium officinale* R. Br.)
Rorippa obtusa (Nutt.) Britton var. *sphaerocarpa* (A. Gray) Cory.
Myriophyllum heterophyllum Michx.
Lippia lanceolata Michx.
var. *recognita* Fern & Grisc.
Myriophyllum proserpinacoides Gill.
Lippia incisa (Small) Tidestrom.
Mentha spicata L.
Utricularia gibba L.
Cyperus erythrorhizos Muhl.
Cyperus ovularis (Michx.) Torr.
Kyllinga pumila Michx.
Scirpus validus Vail.
Scleria sp.
Heteranthera limosa (SW.) Willd.
Juncus diffusissimus Buckl.
Juncus setaceus Rostk.
Juncus tenuis Willd.
Polygonum incarnatum Ell.
Polygonum punctatum Ell.
Polygonum cristatum Englem. & Gray.
Hibiscus militaris Cav.
Monniera rotundifolia Michx.

Lake Worth has approximately fifty-four different species of higher aquatic plants. The portion of the lake area covered by vegetation amount possibly to 8% or 9%, depending upon the time of year and the water level. The quantity of vegetation in Lake Worth is greater than that of the other bodies of water, and the quality is slightly in excess of that found in Lake Dallas. The encroachment of aquatic vegetation does not appear to have been sufficient to cause a reduction in the shore line. Sufficient open areas are found in Lake Worth, and much of the region covered by vegetation has either a sandy or a gravel bottom. If vegetation should be as useful as is often indicated, this lake appears to possess an optimum for the production of plankters, redds of spawning fish, zones of protection for young fry, and general feeding areas.

ANNOTATED LIST OF LAKE WORTH VEGETATION

Nitella sp.
Rorippa nasturtium-aquaticum (L.) Schinz & Thell. (*Nasturtium officinale* R. Br.)
Potamogeton americanus Cham & Schlecht. (Potamogeton lonchites Tuckerm.)
Alisma subcordatum Raf.
Sagittaria graminea Michx.
Azolla caroliniana Willd.
Equisetum hyemale L.
var. *robustum* (A. Br.) A. A. Eaton (Equisetum prealtum Raf.)
Potamogeton pectinatus L.
Echinodorus cordifolius (L.) Griseb.
Sagittaria arifolia Nutt.
Paspalum floridanum Michx.
Paspalum stramineum Nash.
Carex Blanda Dewey
Carex Davisii Schwein & Torr.

Carex microdonata (Torr & Hook.) var. *latifolia* Bailey
Cyperus erythrorhizos Muhl.
Fimbristylis autumnalis (L.) R. & S.
Scirpus validus Vail.
Fuirena simplex Vail.
Eleocharis caribaea (Rottb.) Blake
Lemna minor L.
Juncus bufonius L.
Juncus effusus L. var. *solutus* Fern. & Wiegand
Juncus marginatus Rostk. var. *setosus* Coville (Juncus setosus (Coville) Small.)
Juncus texanus (Englem.) Coville
Juncus tenuis Willd.
Polygonum incarnatum Ell.
Polygonum pennsylvanicum L.
Rorippa nasturtium-aquaticum (L.) Schinz & Thell. (*Nasturtium officinale* R. Br.)
Hibiscus militaris Cav.
Ammannia coccinea Rottb.
Paspalum pubiflorum Rupr.
Zizaniopsis miliaceae (Michx.) D. & A.
Carex crus-corvi Shuttlew.
Carex emoryi Dewey
Carex vulpinoidea Michx.
Cyperus rotundus L.
Scirpus validus Vail.
Fuirena hispida Ell.
Heteranthera limosa (SW.) Willd.
Juncus diffusissimus Buckl.
Juncus setaceus Rostk.
Salix nigra Marsh
Polygonum lapathifolium L.
Nelumba lutea (Willd.) Pers.
Hibiscus trionum L.
Bergia texana (Hook) Seubert.
Ammannia auriculata Willd.
Hydrocotyle verticillata Thunb. (Hydrocotyle cuneata C. & R.)
Lippia lanceolata Michx. var. *recognita* Fern & Grisc.
Lippia incisa (Small) Tidestrom.
Mentha spicata L.
Utricularia gibba L.
Monniera rotundifolia Michx.

Net Plankton

General

The statistical study of net plankton has been in progress for over two years. No attempt has been made on the part of the writers to give the specific identification of the plankters, although such work is in progress. Generic determinations, included in Figs. 5 and 6, indicate that approximately fifty different forms of plankton have been found in the various lakes examined.

Bridgeport, the youngest of the group, has shown a poor qualitative and quantitative distribution of organisms, with the exception of the month of March, 1938. During this month there was a "bloom" of Aphanizomenon, when the count averaged 73,000 filaments to the liter. Melosira also increased at the same time to an average of 50,000 filaments to the liter. The later winter or early spring in Bridgeport has always shown a great increase in the phytoplankters, the duration of the population being generally about three months, followed by a decrease in the late spring and almost depletion in the late summer. The fall may show a slight return followed by a decrease, and then the annual winter increase. The quality is not found in this lake as in

the others studied, the zooplankters never reaching a quantity comparable with the phytoplankters.

It is interesting to note from Figs. 5 and 6 that the occurrence of organisms in Bridgeport is sporadic and that they are not as continuous as those found in the other lakes. The writers are unable to explain these phenomena in the light of the present work. Larger plankton samples, often taken by dragging a net through the water, or in deeper water with a closing net, failed to give more qualitative data concerning the various plankters. Since Bridgeport is more subject to density currents, it may be that there is some relation between the various organisms and turbidity, although this fact cannot be shown from the present work.

The gravimetric studies do not agree in all parts of the work with the statistical data. It should be clearly stated that the writers do not have as much gravimetric as statistical data, since the study was begun in October of 1937, making possible an eight-months' set of readings. During the period from October through May, the dry weight of net plankton varied from 1,360 milligrams per cubic meter to 4,080, the average being 2,589 milligrams. The organic matter in the net samples varied from 102 to 1,110 milligrams per cubic meter, the average being 823 milligrams. The ash content in the sample varied from 60.2% to 75.1%, the average ash content being 67.6% (Table 3).

Statistical data from Eagle Mountain show that net plankters are more prevalent in the annual distribution, both qualitatively and quantitatively. As in most lakes there is a slight rise in net plankters in the fall, particularly in November, which is followed by an increase in the winter to a spring maximum that lasts over a period of some three months. This is followed by the summer minimum. The quantitative differences in the various months can

EXPLANATION OF THE NET PLANKTON DIAGRAMS

The statistical or numerical results shown in Figures 5 and 6 follow the same diagrammatic representation used by Birge and Juday (1922), taken from Lohmann (1908). In this spherical type curve, the radius (r) is so determined that $V = \frac{1}{2^{12}} N$, where V is the volume of the sphere in cubic millimeters and N is the average number of individual organisms per cubic meter of water. Since $V = 4r^3$ approximately, we obtain $r = \frac{1}{16}\sqrt[3]{\frac{N}{4}}$. Thus the number of organisms per cubic meter is given by $N = 2^{14} r^3$.

LIST OF PLANKTON WITH KEY

B—Bosmina, D—Daphnia, Di—Diaphanosoma, P—Polyphemus, C—Cyclops, Ca—Canthocamptus, Da—Diaptomus, Nu—Nauplii, A—Anuraea, As—Asplanchna, Br—Brachionus, Co—Conochilus, Mo—Monostyla, No—Notholca, Ph—Philodina, Po—Polyarthra, Pt—Pterodina, R—Rattulus, Sy—Synchaeta, T—Triarthra, Tm—Tetramastix, Ac—Actinosphaerium, Ar—Arcella, Cm—Ceratium, Df—Difflugia, El—Elvirea, Eu—Euglena, In—Infusoria, Pa—Paramecium, V—Vorticella, An—Anabaena, Aph—Aphanizomenon, L—Lyngbya, Ns—Nostoc, O—Oscillatoria, Cl—Closterium, Dy—Dictyosphaerium, Mg—Mougeotia, Oe—Oedogonium, Pd—Pediastrum, St—Staurastrum, Sg—Spirogyra, Tr—Trochiscia, U—Ulothrix, F—Fragilaria, Gy—Gyrosigma, M—Melosira, Nv—Navicula, Pu—Pinnularia, Sn—Synedra, Ta—Tabellaria, Os—Ostracoda.

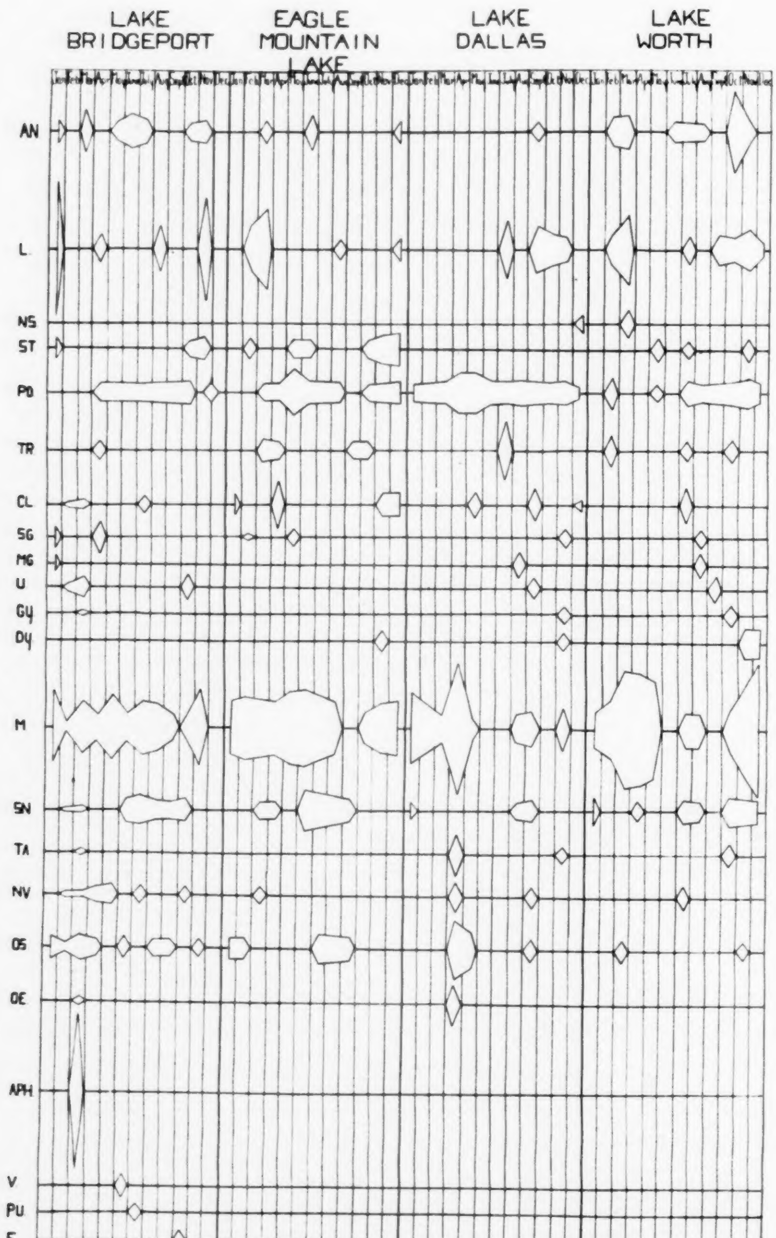

FIG. 5. Diagrams showing average annual net plankton, 1936-1938 inclusive.

See explanation at bottom of page 131.

be attributed more to Melosira, Lyngbya, and a heterogenous group of Rotifera, than to any of the other organisms. Figures 5 and 6 show a rather large group of Cla/locera and Copepoda, with an admixture of green algae. The number of representative Genera was much greater throughout the en-

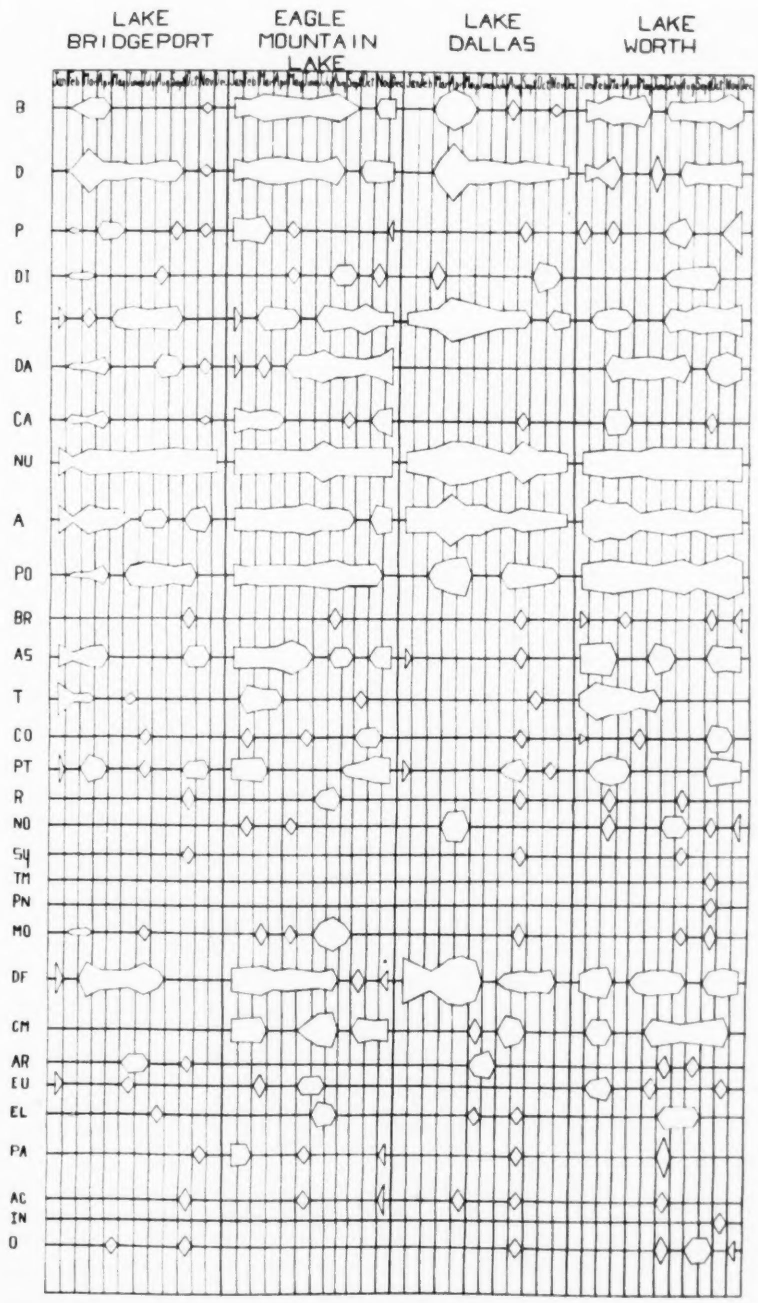

FIG. 6. *(Figure 5 Continued)*

tire year in this lake than in Bridgeport, and the annual productivity of the net plankters statistically showed an increase. The summer decrease is largely due to the fact that diatoms, blue greens, and rotifers become sparse in the upper waters of the lake: the lower waters being stratified, would not permit an excessive growth of plankters.

The gravimetric determination of net plankters (Table 3) showed a dry

weight from 1,020 to 2,820 milligrams per cubic meter, the average for a period of eight months being 1,766 milligrams. The organic matter in the net plankters varied from a fall minimum of 530 milligrams per cubic meter to a maximum of 1,950 milligrams. The average amount of organic matter in the net plankton for an eight-months' period was 1,082 milligrams per cubic meter, which is somewhat higher than in Bridgeport. The ash content in the sample varied from a minimum of 28% to a maximum of 60.8%, the average ash content being 42%.

When studied statistically, Lake Dallas shows a greater annual productivity of plankton than does Eagle Mountain, although the gravimetric data do not support these findings. The month of January is rather low both qualitatively and quantitatively, excepting in the diatom Melosira, which after this month begins to increase. This increase in Melosira is followed in the early spring by a rapid increase in the green algae, which reaches its maximum in the month of March. Possibly the greatest number of mixed plankton forms are found in April, when the zooplankters begin increasing rapidly. Cladocera and Copepoda rise to a rather high concentration, coincident with the decrease in phytoplankters. As summer gets under way, all of the organisms are noticeably reduced, both qualitatively and quantitatively, until in September or early fall, when there is a rapid rise in the Rotifera accompanied by some green algae, which lasts for a few weeks. The winter minimum lasts until the month of January, when the diatoms again begin their increase.

The gravimetric findings show that the minimum of dry net plankton amounted to 1,900 milligrams per cubic meter, whereas the maximum amounted to 3,900 milligrams. The average dry plankton for an eight-months' period for the entire lake was 2,670 milligrams per cubic meter. The organic matter was lower in proportion in Lake Dallas, possibly due to the extreme turbidity of the past ten months, caused by excessive wind and rain. The conditions here more closely resemble those found in Bridgeport in the gravimetric findings. The minimum organic matter was 690 milligrams, and the maximum 870 milligrams per cubic meter. The average amount was 775 milligrams per cubic meter. The ash content varied from 64% to 77%, the average being 68.7%.

Of all the lakes examined, Lake Worth has consistently shown the greatest qualitative and quantitative statistical plankton. Not only is the annual crop greater, but also more prominent forms are to be found in this lake at almost any time during the year. The spring maxima are due largely to Melosira, Anuraea (Keratella), Polyarthra, Daphnia and Bosmina. The fall maxima are due largely to Cyclops, Diaptomus, Anabaena, Lyngbya, Pterodina, Conochilus, Asplanchna, Polyarthra, Difflugia, and Ceratium. During the summer minima, the quality and quantity decrease. This fact is noted more frequently in the algae than in any other group, although the Rotifera are not so prevalent.

The minimum amount of dry net plankton found in Lake Worth over an eight-months' period was 1,435 milligrams per cubic meter; the maximum was 2,710 milligrams. The average dry plankton for the same period was 1,960 milligrams per cubic meter. The organic material in the net plankton varied from a minimum of 650 milligrams to a maximum of 1,110 milligrams per cubic meter, the average being 834 milligrams. The least amount of ash left after ignition was 53.1%; the greatest amount was 62%; the average ash content was 57%.

From the work thus far, it appears from statistical data that the most productive lake in net plankton is Lake Worth, followed in order by Dallas, Eagle Mountain, and Bridgeport. From the gravimetric data, which as yet is incomplete, it appears that Eagle Mountain is the most productive, followed in order by Lakes Worth and Bridgeport, and Lake Dallas (Table 3).

NANNOPLANKTON

The suspended silt in the lake water prevented statistical work on nannoplankton. Materials removed from the centrifuge were damaged in many cases beyond recognition, or were broken so that accurate counting was impossible. All of the work on nannoplankton presented in this paper was secured by gravimetric methods. It should be further stated that the writers are aware of the limitations of the centrifuge, which has a minimum development of 18,000 r.p.m. The data presented in this section cover an eight-months period, beginning in October, 1937, and running through May, 1938. Each gravimetric sample was run in duplicate, often in triplicate, to assure correct weights. All samples removed from the centrifuge were placed in ignited and weighed fused silica boats, having the trade name of "Vitreosil." They were dried for a period of twenty-four hours in an electric furnace, having a constant temperature of 70° centigrade; then weighed for dry weight; later they were ignited in a Hoskins furnace for one hour at approximately 600°, and weighed again to obtain loss on ignition, which the writers use as organic matter. It would seem probable that some inorganic material may have been broken down by this procedure. Since organic analyses were not made of the materials, accurate statements cannot be made. From inorganic analyses of the samples before and after ignition, there appeared to be little loss from ignition. Had the magnesium content run high in any of the samples, some loss might have been experienced.

Bridgeport showed a minimum organic content of 1,190 milligrams per cubic meter in October, 1937 (Table 4). The maximum organic content was 7,540 milligrams per cubic meter, in May, 1938. The fall maximum occurred in November, with a content of 2,810 milligrams per cubic meter, followed by a decline in January to 1,570 milligrams per cubic meter. The spring maximum was first indicated in March, 1938, with 3,810 milligrams and continued to rise until May. The average amount of organic matter in the nannoplankton for the eight-months period was 3,780 milligrams per cubic

meter. It is interesting to note (Table 5) that the ash content varied from 82.9% to 93.7%, with an average of 89.5%. There appears to be some correlation between the turbidity and the organic matter, that is, in all instances when the organic matter was high in nannoplankton, the turbidity was high, and *vice versa*. More will be written concerning this matter as the other lakes are reviewed.

Eagle Mountain did not show the great variation in organic matter which was shown by the other lakes (Table 4), possibly because of the lack of excessive turbidity; however, accurate statements cannot yet be made concerning this relation.

The minimum amount of organic matter in Eagle Mountain, found in October, 1937, was 830 milligrams per cubic meter, the amount in November was less, followed by an increase to 1,700 milligrams in March, 1938. In April the rise continued to an average of 2,330 milligrams to the cubic meter, and in May the maximum was attained with an average of 4,610 milligrams to the cubic meter. The average amount of organic matter for the eight-months period was 1,840 milligrams to the cubic meter (Table 5). The ash content indicated that the percentage of silt in this lake was small when compared with Bridgeport. The minimum amount of ash occurred in the month of May, with an average of 70.7%; the maximum ash occurring in March, 84.5%. The average ash content in Eagle Mountain was 80.3%, as compared with 89.5 in Bridgeport; the organic matter in Bridgeport was 18% greater, while the ash content was only 10.3% greater. Therefore there exists no direct correlation. (Tables 4 and 5.)

The content of organic matter in the centrifuge samples from Lake Dallas was consistently greater than that taken from the other lakes. The main work on centrifuged material began during the fall maximum, in October, with an average of 3,600 milligrams to the cubic meter (Table 4). There was a continual fall in organic content through January, reaching a low of 1,823 milligrams. The peak of the spring maximum came in March, with an average production of 7,303 milligrams, followed by a slight fall in May to 6,670 milligrams to the cubic meter. The average production of organic material in the nannoplankton of Lake Dallas for a period of eight months was 4,270 milligrams to the cubic meter of lake water (Table 5).

The ash content varied from a minimum of 77.2% in October to a maximum of 86.3% in May, 1938 (Table 5). The average for the same period was 79.7%. This percentage is slightly lower than that of Eagle Mountain and is not nearly as high as Bridgeport. The organic content of the water in this lake was 56.8% greater than that in Eagle Mountain and 11.4% greater than that in Bridgeport. It appears that turbidity alone cannot account for the high organic content of the nannoplankton, since Lake Dallas has less turbidity than Bridgeport, with more organic matter.

The organic material in the nannoplankton of Lake Worth showed a distinct fall maximum in the month of October, with an average of 6,087 milli-

grams per cubic meter (Table 4), while the following month a minimum was found for the eight-months' period amounting to 987 milligrams. From this time there was little change, until May, 1938, when the spring maximum averaged 6,370 milligrams to the cubic meter. The average production for the eight-months' period was 3,120 milligrams (Table 5). The ash content for the same time varied from 68% to a maximum of 85.6%, the average for the period from surface to bottom being 72.0%.

The amount of organic material in the nannoplankton of Lake Worth (Table 5) was 41% greater than that found in Eagle Mountain, while the material in Lake Worth was exceeded by 15.1% when compared with Bridgeport, and by 26.9% when compared with Lake Dallas. In terms of another average, Eagle Mountain had an organic crop in the nannoplankton (Table 5) which thus far averaged 253.1 kilograms to the hectare (225.9 pounds to the acre) for the entire depth of 14 meters, or approximately 4.99 pounds to the acre-foot. The next in order of amount of nannoplankton was Lake Worth with 297.4 kilograms to the hectare (265.5 pounds to the acre) for a depth of 10 meters, or 8.5 pounds to the acre-foot. Lake Bridgeport showed 680.4 kilograms to the hectare (607.5 pounds to the acre) for the total depth of 18 meters, or 10.3 pounds to the acre-foot. Lake Dallas had 422.6 kilograms to the hectare (377.2 pounds to the acre) for a depth of 10 meters, or an average of 11.6 pounds to the acre-foot (Table 5).

VERTICAL DISTRIBUTION

The statistical studies of the net plankters showed the expected type of vertical distribution. During the early fall, from the time of turnover through the winter, spring, and early summer until the time of stratification, there was slight variation in the distribution, except as altered by the density currents, which is not permanent. During July and August and often into the

TABLE 3. AVERAGE NET PLANKTON.

Depth Meters	Dry Weight mg. per cu. m.	Organic mg. per cu. m.	Ash per cent	Kilograms Per Hectare Organic Matter	Lbs. per Acre Organic Matter	Lbs. per Ac. ft. Organic Matter
Bridgeport Lake						
0 - 6	2,095	765	64.9%	45.9	40.9	2.08
6 - 12	2,547	925	63.6%	55.5	49.5	2.51
12 - 18	3,125	780	75. %	46.8	41.8	2.12
Eagle Mountain Lake						
0 - 5	1,723	1,053	41.6%	52.3	46.7	2.34
5 - 10	1,780	1,140	38.7%	55.3	49.4	3.01
10 - 14	1,797	1,053	45.8%	41.2	36.7	2.23
Lake Worth						
0 - 5	2,072	880	56.8%	35.2	31.4	2.38
4 - 8	1,802	735	58.5%	35.5	26.2	1.99
8 - 10	2,007	885	57.0%	37.7	15.8	2.40
Lake Dallas						
0 - 4	3,900	870	77. %	34.8	31.0	2.35
4 - 8	2,210	765	65. %	30.6	27.3	2.13
8 - 10	1,900	690	64. %	13.8	12.3	1.87

TABLE 4. AVERAGE NANNOPLANKTON EXPRESSED AS ORGANIC MATTER PER CUBIC METER.

Depth Meters	October mgs.	November mgs.	December mgs.	January mgs.	February mgs.	March mgs.	April mgs.	May mgs.	Average mgs.
Bridgeport Lake									
0 - 6	1.190	2.810	.....	1.570	.....	3.810	.....	7.580	3.640
6 - 12	1.470	3.420	.....	1.750	.....	4.300	.....	6.780	3.900
12 - 18	1.770	3.310	.....	1.540	.....	4.385	.....	7.020	3.800
Eagle Mountain Lake									
0 - 5	1.180	.980	1.260	1.090	1.390	1.390	2.290	3.650	1.640
5 - 10	.830	1.040	1.360	1.260	1.220	1.400	2.070	3.550	1.590
10 - 14	2.360	1.000	1.160	1.160	1.250	1.700	2.720	6.620	2.250
Lake Worth									
0 - 4	5.360	.910	1.400	.....	1.860	1.590	.....	3.780	2.480
4 - 8	4.900	1.050	1.830	.....	2.140	1.430	.....	6.780	3.020
8 - 10	8.000	1.000	1.403	.....	1.870	2.210	.....	8.690	3.870
Lake Dallas									
0 - 4	3.200	2.900	2.340	2.000	.....	7.550	.....	6.590	4.260
4 - 8	3.700	3.000	2.370	1.820	.....	7.840	.....	6.860	4.090
8 - 10	3.900	3.300	3.560	1.890	.....	7.520	.....	6.670	4.830

TABLE 5. AVERAGE PRODUCTION OF NANNOPLANKTON.

Depth Meters	Dry Weight mg. per cu. m.	Organic Matter mg. per cu. m.	Ash per cent	Organic Matter Kilograms per Hectare	Organic Matter lbs. per acre	Organic Matter lbs. per Ac. ft.
Bridgeport Lake						
0 - 6	29,996	3,640	87.7%	218.4	195.0	9.9
6 - 12	31,548	3,900	87.6%	234.0	208.9	10.6
2 - 18	41,475	3,800	93.2%	228.0	203.6	10.3
Eagle Mountain Lake						
10 - 5	8,586	1,640	80.9%	82.0	73.2	4.47
5 - 10	8,510	1,590	81.3%	79.5	70.9	4.30
10 - 14	10,676	2,290	78.6%	91.6	81.6	6.20
Lake Worth						
0 - 4	9,712	2,460	74.5%	99.2	88.6	6.7
4 - 8	10,642	3,020	71.6%	120.8	107.8	8.2
8 - 10	12,836	3,870	70.0%	77.4	69.1	10.5
Lake Dallas						
0 - 4	21,050	4,260	79.7%	170.4	152.1	11.6
4 - 8	22,318	4,090	81.2%	163.6	146.0	11.1
8 - 10	21,324	4,430	79.2%	88.6	79.1	12.0

TABLE 6. TOTAL PLANKTON.

Depth Meters	Organic Matter mg. per cu. m.	Organic Matter kg. to per nectare	Organic Matter lbs. per Ac.	Organic Matter lbs. per Ac. ft.	Organic Matter Average lbs. per Ac. ft.
Bridgeport					
0 - 6	4,405	264.3	236.0	11.9	....
6 - 12	4,825	289.5	258.5	13.1	....
12 - 18	4,580	274.8	245.3	12.4	12.7
Eagle Mountain Lake					
0 - 5	2,693	134.6	120.1	7.3	....
5 - 10	2,730	136.5	121.9	7.4	....
10 - 14	3,383	133.7	119.4	8.3	7.6
Lake Worth					
0 - 4	3,360	134.4	121.6	9.3	....
4 - 8	3,755	150.2	138.1	10.2	....
8 - 10	4,755	95.1	84.9	13.0	10.38
Lake Dallas					
0 - 4	5,130	205.2	183.2	13.9	....
4 - 8	4,855	194.2	173.4	13.2	....
8 - 10	5,120	102.4	91.4	13.9	13.66

early part of September, there is a condensation of plankters in the epilimnion, just above the thermocline, with a great reduction in the hypolimnion. Complete treatment of this subject is not necessary, since the summer season very well agrees with that of temperate lakes of the second order, while the fall, winter, and spring seasons agree with those of temperate or tropical lakes of the third order. Welch (1935) gives a good summary of conditions found to agree with those of the Texas Reservoir lakes.

The vertical distribution of the nannoplankters is apparently less variable. In Bridgeport, the middle region of the lake, 6-12 meters, usually has the maximum production. At the time of density currents, organic matter often accumulates near the bottom, a condition which is temporary.

In Eagle Mountain it appears that the bottom regions are most productive, the surface being next in organic content, and the middle section, 5-10 meters, the least productive. This condition is variable, but the average of all organic matter indicates the condition as described above. Lake Dallas shows the same vertical distribution of organic material as Eagle Mountain.

Lake Worth appears to have a gradual increase in nannoplankton from surface to bottom. It may be in older lakes with heavily silted beds that the agitation by winds brings back into suspension partially deteriorated inundated materials. In any event, the older lakes appear to have more suspended organic matter near the bottom, while the middle section in various months exceeds the upper area, or the reverse is the circumstance.

TOTAL PLANKTON

The gravimetric data for both net and nannoplankton are summarized in Table 6. The most significant figure relating to each lake appears to be the dry weight of the organic material per average acre-foot for the entire lake. It is immediately discernible that Eagle Mountain with an average of 7.8 pounds to the acre-foot, over a period of eight months shows the least amount of total plankton. Lake Worth follows, with 10.38 pounds to the acre-foot; then Bridgeport with 12.7 pounds to the acre-foot; and finally, Lake Dallas with 13.66 pounds per acre-foot.

DISCUSSION

It appears from this investigation that the biological productivity of an artificial lake is as individually variable as that of a natural lake. It appears that age is only one of the many factors governing general biological productivity.

An artificial lake which may appear to support ample net plankton for sustenance of fish is often less productive than one which yields very few net plankters. It is questionable whether the organic materials present may serve as fish food, since the actual chemical composition of the materials is unknown. Therefore, the application of the biological productivity as presented in this paper is of limnological importance, and not intended to convey

the idea that all organic matter is readily usable by fish. The relative food value of the diverse materials will depend on further studies.

As indicated by Raymond (1937), it would appear that a greater amount of aquatic vegetation should be conducive to growth and reproduction of total plankton. It has been found that Lake Worth, which is the oldest, supports less total plankton than either Lake Dallas or Bridgeport, although the difference is not great. It is apparent that Lake Worth under normal conditions has the greatest annual crop of net plankters, but not of nannoplankton. It would, therefore, not appear that Lake Worth is the most productive, even though it does possess far more vegetation than either of the younger lakes and a slightly greater per cent than Lake Dallas.

The amount of silting is no doubt of great importance in determining favorable or unfavorable biological conditions. Ellis (1936) and Moore (1937) indicate that aquatic habitats may be greatly altered by this factor. Eakin (1936) shows that Lake Worth has the greatest silting, although it is obvious that the vegetation has not been greatly hampered, and the net plankton exceeds that of other lakes with less silting. Lake Dallas shows less silting than Lake Worth, although the time factor may play a very important part in this process. More vegetation and net plankters are found in Lake Dallas than in either Bridgeport or Eagle Mountain, and the total plankton here exceeds that found in other lakes. In the deeper lakes it would appear that silting might be beneficial in cutting out profundal zones, and making the entire basin of the lake littoral and sublittoral, as has been accomplished in both Lake Dallas and Lake Worth, but which has not yet occurred in the younger lakes. Since the feed streams have basins composed almost entirely of alluvial soil, this rich material if deposited in shoal regions would greatly enhance the growth of aquatic vegetation and should contribute to plankton production.

In artificial lakes with a large watershed, much of the silting is not produced by clay or sand, but rather by animal and plant remains, inundated from the surrounding areas. It would seem that this material might add to the productivity of the lake, if not in too great abundance. Naturally such materials cannot be called silt, but rather should be referred to as "filling-in" substances, since most of them undergo either putrefaction or decay, and ultimately give up the space in the basin that they occupied.

Since turbidity in the water is more or less an index to the rate of silting or "filling-in," it would appear that the more constantly turbid waters would tend to smother all life, and carry much useful material to the bottom that would not be recovered. Certain workers have voiced this opinion, and scattered references in literature allude to turbidity in water as a very destructive factor. Serious consideration as to what constitutes the turbidity should be given before it is condemned. The writers have found the more turbid waters to contain more organic matter than the less turbid over a long period of time, although a sudden appearance and disappearance of this condition is

unfavorable. Much more work must be done in artificial lakes on the problem of turbidity before really accurate statements can be made. It is not safe to assume that organic material in the turbid waters is wholly usable to fish or to larger invertebrates. This should be determined by stomach content studied on the species in question.

Many opportunities are offered for the study of vertical distribution of phytoplankters in turbid artificial lakes. In many instances the maximum concentration of these organisms is found at a depth of from five to eight meters in water with a turbidity of 100 p.p.m. The authors are uninformed as to the depth of light penetration in these waters but it appears that there is sufficient light to bring about the continued growth of certain diatoms and a blue-green algae, Aphanizomenon.

The total amount of organic material in the water of the artificial lakes in this area of Texas agrees surprisingly with that found by Birge and Juday (1922) in certain Wisconsin lakes. It will be necessary to continue this research for several years before definite statements regarding artificial lakes can be made. The writers have not intended that this paper indicates exhaustive study of this condition, but serves as an index of what one may expect in this area of the Southwest.

It is probable that the sub-tropical climatic conditions of this area will reveal many conditions not unlike those found by Wright (1937) working on certain Brazil reservoirs. The variations in temperature in this region, however, are greater than experienced in Brazil. Most of the Texas reservoirs are larger. The chemical conditions of the Texas lakes, however, are more in agreement with those of the natural type found in the North and the Middle West.

As far as the data from the present lake investigation can be interpreted, it would appear that aging in years is not coincident with "aging geologically." The older lakes appear to be as productive limnologically as those of more recent construction, and in some cases more productive. Present work in progress on bottom fauna, organic analyses, fish growth studies, fish food, and fertilizing of reservoirs should yield more convincing results than the writers can give at the present time. It might be stated from very scanty creel counts or creel census that the younger lakes in this area are much more productive from the standpoint of the angler than are the older lakes. The condition is thought to be due not so much to the lack of favorable conditions for fish growth and reproduction as to depletion of large fish by overfishing.

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